The Axis Deer in Hawaii

BY

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(With two maps, fourteen plates, and seven figures)

CONTENTS

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Abstract

A study of the physical characteristics of the axis deer [*Axis axis* (Erxleben), 1777], introduced into the Hawaiian Islands in 1868, shows no changes in weight and measurements from those of India and Ceylon although it has been isolated for almost 100 years. Tooth development and aging characteristics have been worked out. Upper canines are present at birth but are lost before the animal is a year old. Other physical characteristics are described and discussed in detail.

The reproductive cycle is found not to have changed from that of Indian axis deer. Peak fawning periods are November, December, January, and February. Fawns are produced during all months of the year. Males are sexually active during all months of the year and regardless of the stage of antler development. The majority of bucks are in full rut during June and July. Foetal development, weights, measurements, and methods for aging the foetus are presented in detail; also charts of the reproductive cycle and other aspects of reproduction.

A study of behaviour shows the beginning of a harem system similar to that in members of the genus *Cervus*. The rutting behaviour is typified by a highly ritualized behaviour pattern, both as individuals and towards other males. Posturing by dis-

playing facial expressions and body attitude seems to be related to territorial behaviour and territorial signpost behaviourisms.

The general behaviour as individuals and as a group in relation to types of cover and distances from cover is significant. The animals avoid extensive open areas as well as extensive closed forests. The behaviour of the animals by day and by night is discussed in relation to crop damage with possible significance and its meaning.

Introduction and Acknowledgement

The axis deer was, so far as can be determined from existing records, introduced into the Hawaiian Islands in 1868. These records, based entirely on several newspaper accounts, mention only eight animals, three bucks, four does, and one fawn. The various versions of the arrival of these deer and their subsequent release on Molokai Island are well documented by Cooke (1949). The entire stock of deer on both Molokai Island and Lanai Island dates back to this one introduction of eight deer. Lanai received a stock of 12 deer in 1920. There is some question about the total number of deer transplanted to Lanai but there is no question of the source of the deer, Molokai Island (Cooke 1949). From where or when the present remnant population of axis deer on Oahu Island was introduced is not known. It is possible that deer were brought from Molokai, possibly from other sources.

The most important point, however, is that on Molokai and Lanai the entire population of deer, estimated today at a total of 5000 to 6000 head, is the progeny of only eight animals. This should provide some interesting food for thought for those sportsmen who persistently contend that inbreeding degrades our game species—or rather that the deterioration of a stock of game is due to inbreeding.

As will be seen from our study, there has been no deterioration, physical or otherwise, in the Hawaiian deer herds. No one knows how many deer have been produced since 1868 on Molokai and Lanai. On several occasions, once on Lanai and once on Molokai, there was a determined effort to exterminate the entire deer population. Cooke (1949) quotes figures which give some idea of the tens of thousands that were slaughtered. It is a well-known fact that deer have been hunted continuously and hard during their entire existence on the Islands. All the evidence that we have been able to find, both from the past and during our present study, shows that the axis deer of Hawaii today is in every respect the equal of the Indian axis deer, both as compared with past measurements and present ones.

The habitat of the Hawaiian axis deer ranges from semi-desert types at altitudes generally below 1500 ft. to rain forest at the higher altitudes, reaching rainfalls of over 200 inches at 3000 to 4000 ft. The lower dry habitat is primarily an open savanna-type acacia forest, primarily kiawe or Algaroba (*Prosopis chilensis*) with an understorey of Lantana (*Lantana*

camara) and Ilima (*Sida fallax*) and a variety of grasses, primarily the native Pili grass (*Heteropogon contortus*). The rain forest habitat consists primarily of mixed fern and Ohia (*Metrosideros* sp.) forests and various native and introduced grasses. While many parts of this forest present dense growths of shrubs and ferns, other parts are open glades and open park-like forests of the giant tree fern (*Cibotium* sp.).

In all cases, both dry habitat and wet, the deer are found in semi-open habitats or where dense forests are liberally interspersed with glades and meadows. The affinity for such habitat will be discussed in greater detail under behaviour.

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PHYSICAL CHARACTERISTICS

Axis axis (Erxleben) 1777

Type locality. Banks of the Ganges, India.

Flerov (1952) places this deer in the genus *Cervus* on the basis of morphological affinities and characteristics. In this respect our observations, on the basis of morphological characteristics, field characteristics, and habits, agree with his conclusions.

General Description and Measurements

In general appearance a small cervid, mature males standing about 36 in. at the shoulder, females about 30 in. ; males with antlers ; manes lacking ; colour fawn or tan with persistent white spots ; colour dimorphism weak and irregular. Antlers grow from high pedestals, rounded in cross section, and only lightly roughened near lower quarter ; beam simple, strongly concave in outline and sharply inclined backwards at a point just above the pedestal.

Measurements in millimetres of typical mature specimens are as follows :

Mature male collected 25 March 1958, Molokai Island, west end : Total length 1780 ; tail 280 ; hind foot 440 ; ear 135 ; height at shoulder 935 ; weight : live 156, dressed 116 lb.

Mature female, collected 9 Feb. 1958, Molokai Island, west end : Total length 1640 ; tail 265 ; hind foot 375 ; ear 125 ; height at shoulder 750 ; weight : live 105, dressed 70 lb.

Graf : Axis Deer

Family group. Doe with yearling daughter and current fawn
The terraine and vegetation is typical of the dry parts of Lanai and Molokai Islands.

(*Photo : Lyman Nichols*)

Graf : Axis Deer

Typical axis doe

Note comparatively thin neck and lack of dark colouring on neck and face. Terraine is typical of the steep gulches on Lanai and Molokai Islands.

(*Photo : Lyman Nichols*)

Largest male measured was from the west end of Molokai Island, taken 9 Jan. 1958 : Total length 2070 ; tail 300 ; hind foot 430 ; ear 144 ; height at shoulder 1000 ; weight : live 215, dressed 170 lb.

Largest female was taken on Lanai Island, 29 Oct. 1957 : Total length 1660 ; tail 274 ; hind foot 405 ; ear 129 ; weight : live 120·5, dressed 88·5 lb.

On the basis of condylobasal length, Pocock's (1943) specimens show a greater size in males. His male axis skulls all range from 260 mm. to 302 mm. with most of them in the upper limits. The largest buck collected in Hawaii, an old buck estimated at 8-9 years old, had a condylobasal length of 293 mm. Pocock's males may have been specimens collected by hunters, who tend to select older, trophy-sized animals. His female skulls show a range from 231 mm. to 260 mm. These compare favourably with Hawaiian skulls which ranged from 216 mm. to 265 mm. Eight fully matured does, i.e., two years or older, averaged 244 mm.

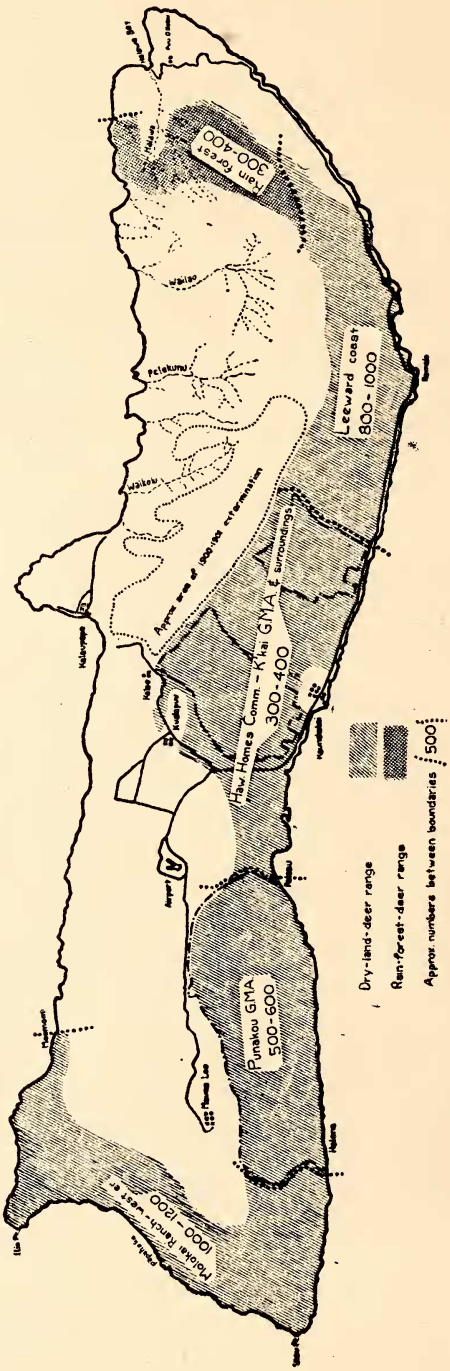
Phillips (1935) lists the average of 9 Ceylon males and 3 females.

Males : Total length 1420 ; tail 283 ; hind foot 392 ; ear 156 ; height at shoulder 831 ; weight (of 5 only) 162 lb.

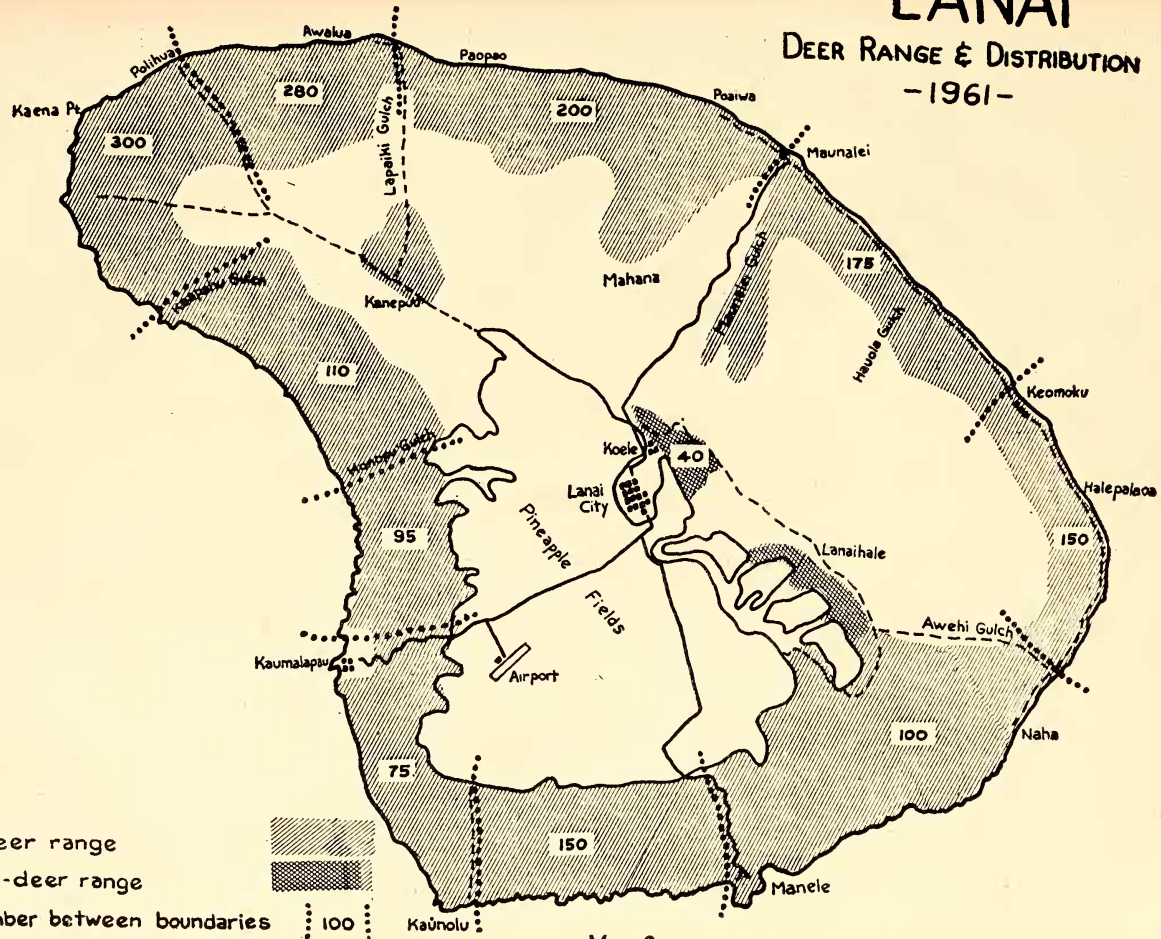
Females : Total length 1283 ; tail 177 ; hind foot 301 ; ear 115 ; height at shoulder 698 ; weight 109·3 lb.

If these measurements are representative, it would appear that Hawaiian deer do not differ greatly from the Indian. Pocock's female skulls bear this out and, although his male skulls are larger, the uniformity and measurements near the upper limits indicate selective collecting—as could be expected when skulls are obtained from sportsmen. Our Hawaiian skulls are, however, close enough to be comparable. The Ceylon measurements would indicate that the deer there are somewhat smaller if the averages given are from representative mature deer. The largest listed had a total length of only 1701·8 mm., a measurement more nearly that of our average (table 3) of 1781 mm. These discrepancies could very well be in the method of taking measurements. The axis deer has apparently lost none of its characteristics during more than 90 years of isolation and inbreeding from four original pairs.

These deer are considered the most primitive representatives of their group today, as shown by various morphological characteristics. These characteristics are particularly the high bony pedicles from which the antlers grow, the simple antler structure with only a basal brow tine and a simple upper tine always on the inside of the beam, the weak and inconsistent colour dimorphism, and the strongly spotted coat which is persistent throughout life. The weakly developed herding and harem characteristics for a member of this group probably also can be added to this category.


MOLOKAI
DEER RANGE & DISTRIBUTION
- 1961 -
Rain forest 300-400
Leeward coast 800-1000
Hav Homes Comm - Kaiser GMA & surroundings 300-400
Punakou GMA 500-600
Molokai Ranch - west of 1000 - 1200
Dry-land-deer range
Rain-forest-deer range
Approx numbers between boundaries 500

MAP 1


LANAI
DEER RANGE & DISTRIBUTION
-1961-
Awalua
Paopao
Polihua
Kaena Pt.
280
200
300
Lapaiki Gulch
Poaiwa
Maunalei
Mahana
Kanepuu
175
Maunale Gulch
Hauola Gulch
Keomoku
110
Koele
40
Lanai City
Halepalaoa
95
Pineapple Fields
Lanaihale
150
Awehi Gulch
Kaumalapau
Airport
100
Naha
75
150
Manele
Kaunolu
Dry-land-deer range
Wet-forest-deer range
Approx. number between boundaries
100

MAP 2

In outline the axis deer quite strikingly resembles a small elk or wapiti, with its high shoulders, thin neck, and rather long face which in shape and outline strongly resembles that of its large relative. In general the body is well-knit and graceful in appearance. Does with their thinner necks appear a bit ungainly about the head, somewhat after the manner of a cow elk, thus heightening the resemblance between these two groups even more. Bucks present a better balanced and more pleasing appearance to the eye, particularly during the rut when the necks are enlarged. Young bucks or even old ones, when the necks are still normal in size, show a tendency toward the same ungainliness observed in does, though not to the same extent.

Colour

All points considered, the axis deer probably rates as one of the most beautiful of all deer. The ground colour of the coat is generally a light reddish brown or yellowish brown. In the males the neck and foreshoulders may be darker, almost charcoal, and in one or two this part was observed to be a lighter yellowish or light fawn colour in contrast to the rest of the body. Females never show this darker colour. The entire dark part of the body is covered with snow-white spots about 20 to 25 mm. in diameter. These are arranged roughly in rows parallel to the mid-dorsal line and across the lower hips, flanks and shoulders ; on the neck up to the head and elsewhere, the spots are more or less arranged at random, but may at times take the form of broken rows.

The outer legs are without spots and the chest, belly, and inner legs, and at times the outer, lower legs, are pure white. A white throat patch extends from about half way up the throat and along the lower jaw to end just below the nostrils. The white of the belly and inner hind legs continues in a narrow band between the buttocks and along the under surface of the tail.

A dark chocolate-brown to blackish brown band extends along the mid-dorsal line from about midway of the neck to the rump ; within this band and on each side of its center line is a row of white spots. The upper side of the tail is light brown bordered with darker brown hairs where it joins the white under surface. A thin line of dark brown hairs splits the white of the chest from the lower throat down the brisket. The white spots on the neck give way to a solid light brown on the head, face, and back of the ears. The edges of the ears are rimmed with dark hairs, while the inner surface of the ears is white near the base.

Does are generally slightly lighter in colour than bucks, especially over the face and neck. Bucks have a black or dark brown diamond-shaped spot in the middle of their forehead and a black line that extends from the antler base to the eyebrow on each side of the head, and con-

Graf : Axis Deer

Three large axis deer bucks, Lanai Island, Hawaii

(*Photo : Lyman Nichols*)

tinues from the eyebrow to the bridge of the nose, thus forming a black inverted chevron on the face. The black may or may not continue down the nose to the muzzle, but there is always a black band that runs from the rear of the mouth forward and over the muzzle just behind the nostrils. The ground colour of the head and face is lighter brown than the body, while the naked portion of the muzzle is grey in colour. Does occasionally have dark faces, but the black chevron and nose band are not present.

Bucks often have darker necks than does. This darkening of the ground colour extends from the front of the shoulders to the head and is highly variable, from just a very slightly darker brown to almost charcoal black. On Molokai it was most pronounced during late summer and fall in bucks with fully hardened antlers. Bucks in shed or velvet condition appeared more uniform in colour. The dark necks were also more pronounced on the leeward side below Mauna Loa, some here having the almost charcoal black necks. This was also the area where one melanistic buck was seen.

No colour difference was observed between the deer of the high wet forest and the dry lowland areas although hunters claimed that deer were darker from the swamps of the high cloud forest.

Antlers take on the characteristic colour of the substances with which they come in contact when rubbed, and antler colour may vary greatly from range to range.

Melanism and Albinism

Melanism, i.e., an all black colour, is rare in deer. It was observed in one buck on the leeward side in the Punakau Game Area in 1958. This was a mature buck of better than average size with fully developed, hard antlers. The colour appeared as an overall charcoal black, rather than a glossy black. The white spotting appeared in normal pattern from a distance, but due to cover it was not possible to determine the colour of the underparts. This particular area also has shown the darkest neck colours of any area observed on Molokai. This 'black' colour appeared similar to the black observed in the melanistic mule deer specimens of northern California and Nevada. It was not possible to determine whether any brown hairs were mixed in with the black because of the distance. Lydekker (1893) mentions a black variety. He says : 'there is a rare black variety of the spotted deer, in which the spots are scarcely perceptible.'

Albinism apparently occurs, but is rare. One albino buck was reported seen in the mountainous country east of Kaunakakai, Molokai. Bahadur (1942), reporting on a captive albino, states :

'The original sire has horns about 2 ft. in length with no tines ; they are always

> in velvet, of a pink flesh colour, and the ends appear slightly raw. He drops his horns annually but the new ones grow in the same way.'

He described the albino as having pink eyes, nose, ears, and light coloured hoofs.

Mrs. Marie Palit, of Ranchi, India, in personal correspondence states that she has seen 3 albino fawns in the past 12 years near her home. Two were picked up and died, and the third, three-fourths grown, was seen with a normal coloured doe.

The Coat

The coat is composed of soft, fairly short hair which normally lies flat and gives these deer a very sleek appearance. The hairs are not brittle like those of North American deer and antelope, but are soft and flexible, and the coat is silky to the touch. There is a sparse undercoat of very fine hair beneath the outer coat of guard hair. Sebaceous and apocrine glands are found at the base of each hair shaft, and these exude an oily liquid which makes the coat shine and helps repel water. However, the amount of oil normally exuded is slight, and the coat feels dry and fluffy. On very hot days, though, the secretion is increased and tiny droplets may be seen on each hair, giving the appearance of sweat.

The coat of young fawns is somewhat heavier than that of the adults, but the hairs are finer and fluffier, giving the fawns a fuzzy appearance. The fine silky undercoat is also heavier.

Bucks, at least, have the ability to erect most of the hair on the neck and torso, as well as hair on the tail and of the rump patch. When a buck is threatening another, he will erect the hair over most of the body, particularly that of the white rump patch and the under-tail so that he resembles an angry, fluffed-up tomcat. Does have not been observed to fluff out their whole coat, but they erect the hairs of the rump patch and the under-tail when excited.

The coat is kept clean by frequent licking; in fact, these deer are one of the cleanest of all wild animals that we have observed, and none has ever been observed with a dirty coat unless it had very recently gotten up from a muddy bed.

The seasonal change in the coat is very gradual and, rather than the usual fall and spring moult observed in North American deer, there is a gradual thinning so that in the winter the coat becomes somewhat heavier and again in the summer somewhat lighter. A moult such as can be observed in North American deer could not be detected, and the process of moulting itself was hard to detect at a given time. The one difference that could be noticed, though it was slight, was that during the period when the antlers were shed or in the velvet some of

the bucks did not show the darker neck colour, appearing lighter on those parts.

Antlers

The antlers develop from bony pedicles which rise about one to one-and-a-half inches above the surface of the frontal bone, the antler forming a distinct burr at its base and growing in a line with the axis of the pedicle to a point where the brow tines branch from the beam. At this point the beam bends sharply backward, almost 45° from the original axis for roughly half its length and then bends upward again at nearly a right angle ; this presents a distinctly backswept and concave or dished outline from the plane of the face. The brow tines arise at right angles from the beam and grow forward and outward. The main beams turn slightly outward and continue to spread until about the main bend in the beam, then continue more or less parallel during the upward sweep. A single tine branches from the inner side of each main beam near the upper one-fourth of the otherwise unbranched beam. In well-formed antlers the view from the front is an almost perfect lyre shape. Some have very narrow, almost parallel, beams and others very widespread ones, though the latter appears to be less common. The most symmetrical antlers will have a spread of about $\frac{1}{3}$ to $\frac{1}{2}$ their length at the bend of the beam with the tips somewhat closer together. A good set of mature antlers in the 30-inch class makes an interesting and fine trophy, though somewhat plain in its simplicity.

The surface of the antlers is slightly to moderately roughened or veined, with the lower or basal part showing the greatest degree of roughening, and even beading at times. This varies from animal to animal, some antlers being almost smooth, others very rough on the lower $\frac{1}{3}$. A pair of large antlers in the office of the Molokai Ranch is covered over the entire surface of the beams with fine to very coarse beading. These antlers were said to have come from a castrated buck. Although roughened over the lower surface, the antler tips are nearly always smooth, polished, and sharp.

Beneath the drying velvet covering, the newly-matured antler is bone white, but as soon as the velvet begins peeling, blood begins to stain the antler brown. Rubbing against trees, shrubs, and sometimes the ground, continues to darken the stain while the roughened portions of the antler soon become filled with embedded bark fragments and dirt, leaving the antler surface relatively smooth and dark except for the ivory-coloured tips. The objects against which the antlers are rubbed will largely determine their final colour. In the kiawe (*Prosopis chilensis*) forest zone, they are frequently a light to a medium brown, and not uncommonly, a greenish brown colour from the embedded bark and stain. Some may

have a yellowish or reddish cast from the colour of the soil in the area—a soil which readily stains objects.

In the wet cloud forest of Molokai, antlers are so frequently washed by rain and by contact with wet shrubbery that the bark fragments do not have a chance to set into a hard paste, and are usually washed off, leaving the antlers more or less free of debris. They are, however, commonly coloured a dark chocolate-brown from the staining effects of plant juices and blood, and are usually darker than those from the lowlands.

The clean, ivory-white of the tips may result from gouging the antlers into the ground—a habit of some bucks, but may be partly due to the natural smoothness of the bone surface here, which does not take a stain readily nor hold a coating of bark or dirt.

Yearling bucks develop spike antlers that point to the rear like short, sharp daggers. Such spikes may at times be adorned with several short snags at their bases. Second-year bucks may develop a simple beam with brow tines or may develop light-beamed three-point antlers. In these the main-beam tine may be a mere stub or it may exceed the main beam above it. Such antlers usually lack the curving sweep of older bucks.

Antler variations and malformations are common. Bucks are commonly seen with one normal, fully developed antler, and one that is shorter and lacking the upper point, or is twisted and deformed. Some of the defects may be of a hereditary nature, but others are undoubtedly due to injuries sustained while the antler is still young and soft.

Old bucks are occasionally seen with antlers lacking the intermediate or main-beam tine, the main beams forming long curved spears. Such bucks have passed their prime sexually, and, as is common in most deer, antler points decline in number and size after this, the main beam being the last to be affected. Just what this age is is difficult to say. Rudolph, the captive buck on Molokai, grew antlers as large as any previously grown in his 9th year, indicating that he had not yet passed his sexual prime.

Antler Measurements

The largest antlers measured during the study were 37 in. in length along the curve of the beams. These were brought in too late to be included in our tables. There are without doubt larger bucks with better antlers on both Molokai and Lanai.

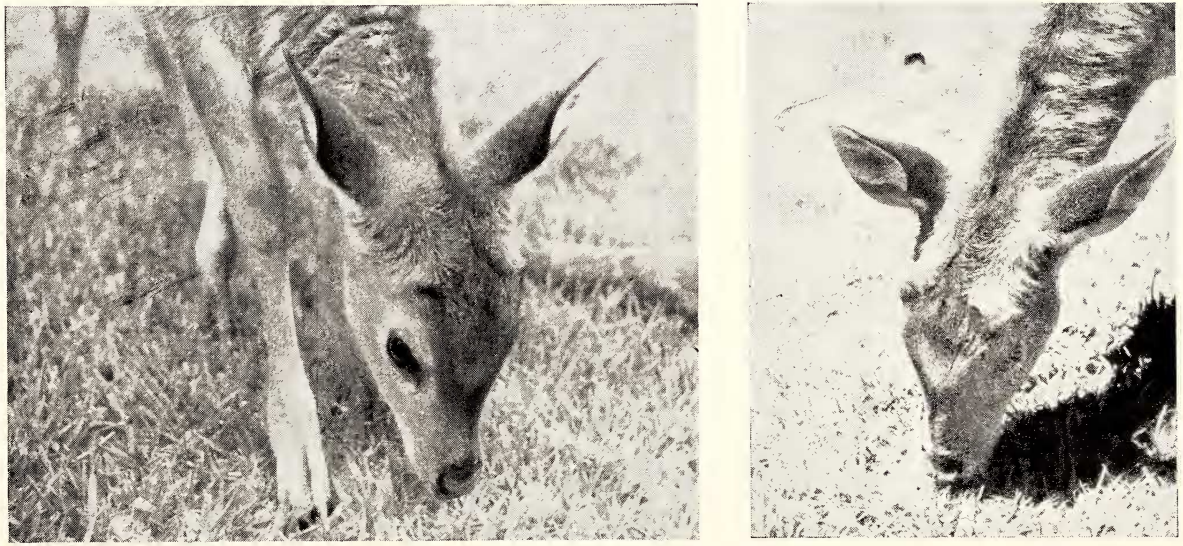
Table 1 lists the average measurements in cm. and inches of all the antlers measured during this study with the exception of spike bucks which are obviously not full grown. The upper and lower ranges of the measurements encountered in the study are also included. The various measurements were analyzed statistically to see if there was any significant

Graf : Axis Deer

Skull of typical, mature axis buck from Hawaii

(*Photo : Lyman Nichols*)

Graf : Axis Deer



Willie, the hand-raised Fawn

Left : At 9 weeks old. Was eating lawn grass in quantity. No sign of antler growth, only dark whorls of hair where antlers would appear. *Right :* At 30 weeks old. Antler growth just beginning.

(*Photos : Lyman Nichols*)

difference between antlers of Molokai and Lanai bucks, but in all cases it was found that there was less than one chance in 100 that there was a real difference noted in the sample of antlers measured between Molokai bucks and Lanai bucks—analysis showed that this was due to sampling error rather than to a real difference in size between the two populations. Consequently, all measurements of antlers of Molokai and Lanai bucks were lumped together and again statistically analyzed to give the data presented in Table 1.

TABLE 1

ANTLER MEASUREMENTS (IN CENTIMETRES) OF ADULT BUCKS
(The numbers in parentheses show the equivalents in inches)

Average Beam Length	
(Length of left and right beams averaged)	
Sample Mean (Average Beam Length)	55·89 (22·00)
Standard Deviation of the Mean	1·46
CI_{99} of the True Mean	52·11-59·66
Sample Range (Shortest and Longest Measurements)	24·2-80·4 (9·52-31·65)
Standard Deviation	12·93
CI of 99·7% of the True Range	17·10-94·68 (6·74-37·25)
Number of Measurements in Sample	79
Average Circumference above the Burr	
(Circumference of left and right beams averaged)	
Sample Mean (Average Circumference)	11·37 (4·48)
Standard Deviation of the Mean	0·03
CI_{99} of the True Mean	11·29-11·45
Sample Range (Smallest and Largest Circumferences)	9·0-15·6 (3·54-6·15)
Standard Deviation	1·55
CI of 99·7% of the True Range	6·71-16·03 (2·64-6·32)
Number of Measurements in Sample	79
Average Circumference above First Fork	
(Circumference of left and right beams averaged)	
Sample Mean (Average Circumference)	8·55 (3·36)
Standard Deviation of the Mean	0·17
CI_{99} of the True Mean	8·11-8·99

Sample Range (Smallest and Largest Circumferences) ..	6·0-12·4 (2·36-4·88)
Standard Deviation	1·46
CI of 99·7% of the True Range	4·16-12·93 (1·64-5·17)
Number of Measurements in Sample	76

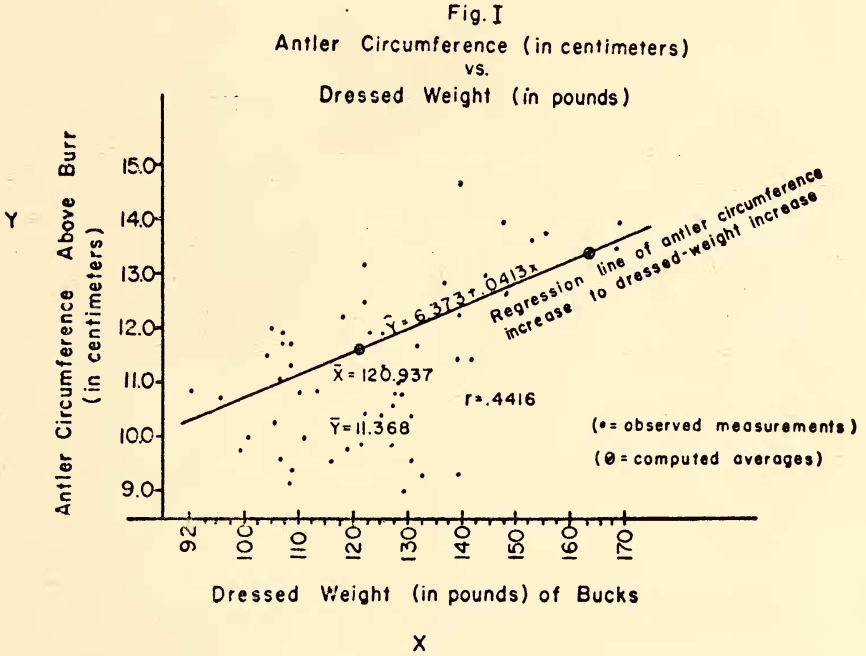
Spread between Tips of Main Beams

Sample Mean (Average Spread)	39·42 (15·50)
Standard Deviation of the Mean	1·21
CI_{99} of the True Mean	36·30-42·55 (14·28-16·75)
Sample Range (Narrowest and Widest Spread)	19·0-70·5 (7·48-27·74)
Standard Deviation	10·44
CI of 99·7% of the True Range	8·10-70·75 (3·19-27·85)
Number of Measurements in Sample	75

Also included in Table 1 are the statistically computed confidence intervals for the means of the measurements. While the averages of the measurements may be determined arithmetically from the samples examined, it does not necessarily follow that the sample average is exactly the same as the true average of all antler measurements. Analysis shows within what limits the true average probably falls. For example the average antler beam length of the antlers measured was found to be 55·89 cm., but statistical analysis of the data shows that the *true* average of all antlers, including the great number not examined, probably falls between 52·11 and 59·66 cm., with less than one chance out of 100 of falling outside of these limits (indicated by CI_{99}).

Analysis of the data also can show the probable upper and lower limits of the measurements of all antlers. Again using the antler-beam length as an example, it may be seen from Table 1 that the shortest antler beam measured was 24·2 cm., and the longest was 80·4. Since only 79 sets of antlers were measured to determine this range, it is reasonable to assume that out of several thousand deer remaining unmeasured some are going to have shorter, and some will have longer, antlers than those examined. Statistical analysis of the sample data indicates that about 99·7% of all bucks on the two islands will have antlers measuring between 17·10 and 94·68 cm. in beam length. Thus we can state that the longest antler length that can normally be found on Molokai and Lanai is probably about 94·68 cm., or 37¼ in.—but of course, there is still a chance that a few rare individuals may exceed this length.

It was noted that antler circumference and beam length seemed to be roughly related to the size of the buck, and these measurements were, therefore, examined graphically and statistically to see if this was truly the case. Examination did show a fair correlation between antler circumference above the burr and the dressed weights of the bucks, and indicated that antlers grow more massive in direct relation to the bucks' increase in weight as demonstrated in Figure 1. Although the general correlation could be computed and shown, individual measurements did not follow the computed average regression line too closely. The correlation of beam length and body weight was very weak and is not illustrated.



It is probable that antler beam circumference, and possibly beam length, are directly related to the age of the buck, getting larger and longer as the buck grows older. Unfortunately the ages of the bucks whose antlers were measured were not known. Until a number of known-age bucks are available, this relationship cannot be determined with certainty. Both food quality and quantity, and heredity are known to influence antler size and could upset the direct relationship between size of body and antler size. Also it could well be that body weight and age of bucks are not closely related beyond a certain point ; hence the weak correlation between antler size and weight.

For those who are interested in the antler measurements of bucks from India and Ceylon, the following will give some comparison :

	Beam Length	*Circum-ference*	*Spread*
India—(Lydekker 1898) ..	38¼	4¾	19½ in.
India—(Rowland Ward 1928) ..	40	4½	23¾ in.
Ceylon—(Phillips 1935) ..	36	4	23½ in.
	36¼		19¾ in.

Any buck with antler beams above 30 in. and a basal circumference of over 4 in. can be considered a good one. It would appear from our measurements that Hawaiian deer have heavier and wider antlers than the Indian or Ceylonese deer.

Weights and Body Measurements

There is a persistent misconception among many people both in Hawaii and among tourists who have visited the Islands, that the Hawaiian deer are small, almost tiny. Expressions such as ' small ', ' tiny ', etc. are often heard. How or why this should be is not known ; certainly the axis deer cannot be listed with the largest deer, neither can it be listed with the smallest. They compare favourably on the average with the well-known white-tailed and black-tailed deer of North America, although the extreme weights of bucks of these species exceed those of the axis bucks that we have weighed. However, in view of our lack of a good sample of large bucks from the high forest of Molokai, this discrepancy may not be as large as it appears to be.

Table 2

Average Dressed Weights (in pounds) of Hawaiian Axis Deer

Adult Bucks	
Sample Mean (Average dressed weight)	120·3
Standard Deviation of the Mean	2·23
CI_{99} of the True Mean	114·5-126·1
Sample Range (Lightest and Heaviest Weighed)	74·0-170·0
Standard Deviation	21·32
CI of 99·7% of the True Range	56·3-184·3
Number of Measurements in Sample	92
Spike Bucks	
Sample Mean (Average Dressed Weight)	88·5
Standard Deviation of the Mean	2·16
CI_{99} of the True Mean	82·5-94·6

Graf : Axis Deer

Willie, the hand-raised Fawn.

Left : At 34 weeks old. Antler development well under way. *Right :* At 51 weeks old. Has well developed velvet-covered spikes.

(*Photos : Lyman Nichols*)

Graf : Axis Deer

Willie, the hand-raised Fawn, at 69 weeks old

Willie's antlers were fully mature at 63 weeks. Here, at 69 weeks the swelling neck, sleeker coat, and filling out of the body show the full masculinization of a buck entering the rut. At this age he was mean and aggressive, constantly looking for trouble and dangerous to humans, whom he no longer feared. The lower picture shows him in the typical attitude and posture of a challenging buck, the attitude and expression during ritual posturing between two bucks.

(*Photos : Lyman Nichols*)

Sample Range (Lightest and Heaviest Weighed)	71·0-109·0
Standard Deviation	10·80
CI of 99.7% of the True Range	56·1-120·9
Number of Measurements in Sample	26

Adult Does

Sample Mean (Average Dressed Weight)	70·5
Standard Deviation of the Mean	1·67
CI_{99} of the True Mean	65·0-75·1
Sample Range (Lightest and Heaviest Weighed)	55·0-97·0
Standard Deviation	9·0
CI of 99.7% of the True Range	45·5-97·74
Number of Measurements in the Sample	30

The average dressed weights (with the viscera removed) of the axis deer examined are given in Table 2. 'Adult bucks' here refers to those larger than spike bucks, which are generally referred to as yearlings. From this table it can be seen that the average weight is 120·3 lb. It was found that the average loss of weight in the field dressing was 24%; thus the average live weight of adult bucks is about 158 lb. The computations indicate that the largest bucks may dress out at as much as 184·3 lb., or weigh when alive up to 243 lb., and possibly more in exceptional cases. The heaviest buck examined during the course of this study had a live weight (whole weight) of 215 lb. and, eviscerated, weighed 170 lb.

It should be pointed out here that weights and statistical conclusions are based on deer collected in the dry-land habitat, with one exception —one buck taken from the Molokai wet forest. This buck, compared with a Molokai buck of the same age class and size from the low, dry-land areas, was found to weigh 10 to 12% heavier. Actually the nearest comparable dry-land buck was slightly larger than the one from the high forest. *If* this difference in weight should prove to be a general rule, then we might expect to find bucks that will go as high as 250 lb. dressed weight in the wet forest area. We have had unconfirmed reports from hunters of weighed bucks in this weight range.

It must also be remembered that the deer of these tropical regions do not put on layers of fat as do northern deer. The best-conditioned bucks that we have examined show almost no subcutaneous fat and only a moderate amount of visceral fat. In contrast, northern-climate deer in good condition put on many pounds of fat in the fall, thus adding considerably to the weight of the animal.

Does are considerably smaller than adult bucks, weighing on the average, only about 70·5 lb. dressed. Since they lose about 31% of their weight upon field dressing, a percentage which varies greatly during pregnancy, an average live doe would weigh about 97·8 lb., an extremely large doe could weigh up to 141 lb.

As a matter of interest, the normally unused portions of one buck were weighed separately to determine what part of the animal's weight they represent. It was found that in this case, the viscera (all internal organs) weighed 25% of the live weight ; the hide 7·2% ; the head 6·6% ; and the feet 2%. The forequarters (separated from the hindquarters between the last two ribs as is usually done) weighed 30·2% of the live weight, and the hindquarters 28·3%. The remaining 0·7% of the weight was accounted for by blood loss.

Weights of Lanai deer appeared to be greater than on Molokai, but statistical comparison again showed no significant difference between the two populations.

TABLE 3

AVERAGE BODY MEASUREMENTS (IN CENTIMETRES) OF AXIS DEER
(The numbers in parentheses show the equivalents in inches)

	Average Length	*Sample Range*
Adult Bucks		
Total Length ..	178·1 (70·25)	164·0-207·0
Tail Length ..	30·9 (12·2)	26·0-36·0
Hind Foot ..	41·8 (16·5)	39·0-45·0
Ear Length ..	13·7 (5·4)	12·0-15·0
Shoulder Height ..	93·2 (36·7)	80·0-101·0
Head Length ..	31·0 (12·2)	29·0-33·5
Spike Bucks		
Total Length ..	162·2 (63·8)	148·5-173·0
Tail Length ..	30·1 (11·8)	26·5-36·0
Hind Foot ..	40·2 (15·8)	31·0-44·0
Ear Length ..	13·3 (5·2)	12·5-14·5
Shoulder Height ..	85·4 (33·6)	78·0-99·0
Head Length ..	28·4 (11·2)	24·0-30·5

		Adult Does		
Total Length	..	155·7 (61·3)	.....	144·0-167·5
Tail Length	..	27·0 (10·6)	.....	20·0-30·0
Hind Foot	..	37·5 (14·8)	.....	35·5-40·5
Ear Length	..	12·6 (5·0)	.....	11·5-13·4
Shoulder Height	..	78·1 (30·8)	.....	70·0-87·
Head Length	..	27·8 (10·9)	.....	24·5-30·0

Various body measurements were also made on deer examined during the study and are presented in Table 3. The total length is the length from the tip of the nose to the tip of the last vertebra in the tail, following the body contours. The tail length is from the tip of the last vertebra in the tail to the junction of the coccygeal and sacral vertebra, and is taken by bending the tail at right angles to the back and measuring from the base to the tip of the tail exclusive of hair. The length of the hind foot is measured from the point of the hock to the tip of the hoof, and the ear length from the notch of the ear (the deepest notch at the inner base of the ear) to the tip. Shoulder height is from the ball of the foot to the mid-line of the back and, though it is slightly longer than the actual standing height, it gives a reasonable approximation of the true height at the shoulder. The head length is from the tip of nose to the notch of the ear. With the exception of the head measurement, which we added for our own convenience, these are standard measurements used in the scientific comparison of animals. They provide a constant standard of comparison which the layman will have little occasion to consider and even less to use.

Glands

The external scent glands of the axis deer are similar to those of other deer. Inter-digital glands are present between the toes of each hind hoof, and are indicated externally by a distinct line of dark hairs. The skin at the opening of these glands is involuted and covered with short, oily hairs, while subcutaneous glandular tissue is abundant. There is a less distinct line of dark hairs between the front toes, but the involuted skin, oily hairs, and glandular tissue are absent or much reduced, indicating a lack of functional glands here. Metatarsal glands are located several inches below the hock on the outside of the metatarsus, or lower hind leg. The glands themselves are small—about three-quarters of an inch long—but are indicated externally by a larger clump of comparatively

long, light-coloured hairs, which are quite apparent against the normally short, brown hair of the leg.

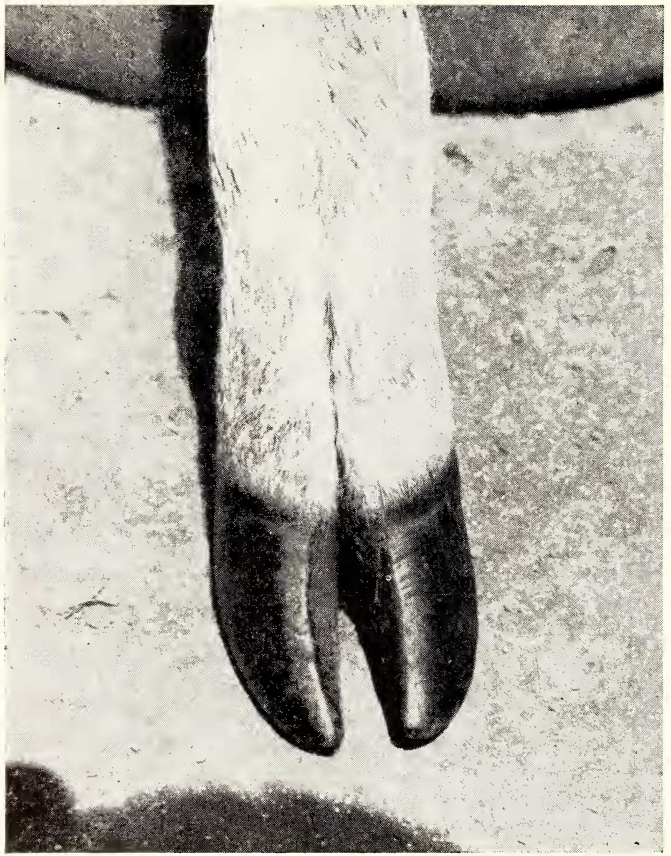
The most noticeable and interesting of the external glands is the infra-orbital gland located just below the inner corner of each eye. This gland normally appears as a mere slit extending from the junction of the upper and lower eyelids. When the deer is excited, however, the gland can be rapidly opened to reveal a large, shallow pouch of nearly the dimension of the eye itself. At the lower, or nostril end, of this gland is a clump of longer oily hairs that are normally folded inwards and enclosed in the slit-like opening. When the gland is flared open, these hairs are rolled outwards, forming an oily tuft at the end of the pouch. This gland appears to be activated by excitement, anger, or other emotional stimuli, and can be opened or closed almost as fast as the winking of an eye. Excitement can be in the form of hunger and anticipation ; when fawns are nursing, or are about to nurse, they become tense with anticipation and their infraorbital glands are flared wide. Or when deer are alarmed, they stand tense and alert, with the glands partially opened.

The glands appear most highly developed in bucks, and appear to be most important when the buck is threatening or challenging another buck, or just stalking around impressing himself with his own importance and toughness. In such instances the glands are opened to their utmost and add considerably to the fierce expression of the face.

Close observation of the captive buck Rudolph, on Molokai, showed that apparently the slightest emotional disturbance or stimulus would cause the glands to open. Obvious stimuli, such as threatening gestures toward the buck or walking close to the fence, caused the glands to flare. Sudden motion towards the buck never failed to bring reaction. Even when standing 10 to 15 feet from the buck, the sudden motion of the hand toward him would cause the gland to open at least partly, and a threatening step forward would usually bring it to full expansion. It was also noticed that even though no threatening gestures were made and the buck had been allowed to become quiet, the gland would at times open partly, sometimes momentarily almost fully, even though no apparent reason was visible.

At this time the antlers were still in velvet, though almost fully developed in size, and the buck's neck was showing some slight swelling, indicating that the emotional state of the rutting condition was building up. Normally, a buck's neck shows no swelling before the antlers are hard, and in North American deer we have never observed neck swelling among bucks still in the velvet. However, a number of axis deer have been observed in the wild state with necks beginning to swell when the antlers are fully grown but still in the velvet. The largest buck collected, with fully grown antlers still in the velvet and slightly rubbery at the tips, showed pronounced neck swelling. This is undoubtedly due to the

Graf : Axis Deer



Feet of Axis Deer

Left : Left front foot. *Right :* Right hind foot

Interdigital scent gland is outlined by dark hairs on hind feet, it does not show on front feet.

(*Photos : Lyman Nichols*)

Graf : Axis Deer

Axis deer, showing infraorbital gland. *Above :* Gland closed, the normal aspect. *Below :* Gland open.

The infraorbital gland, seen here as a shallow pouch in front of the eye, can be opened and closed rapidly under stress of excitement.

(*Photos : Lyman Nichols*)

fact that there is no true sexual quiescence in these deer as there is in northern-climate deer. The physiological condition of the rut, therefore, appears before the antlers are fully hardened and cleaned.

The odour of these external glands is very mild and is a mildly sweetish, musky odour that is not unpleasant. It is hardly noticeable to the human sense of smell except when the glands are held close to the nose. Even old bucks in full rut have little or no odour. There is no comparison with that of a rutting mule deer buck or bull elk.

On damp days, when trailing deer up-wind, they can often be detected as much as 50 yards away by a characteristic pungent odour. This, however, is the odour of the fresh droppings or urine which are almost continuously being deposited by one or other animal in a herd. This odour is somewhat similar to that of the fresh dung of cattle, and is never apparent on the animals themselves.

The genitalia of axis deer are quite similar in appearance to those of other Cervidae, with no significant differences worth recording. The mammaries of the does are equipped with four small teats and two rudimentary accessory teats.

Hoofs and Tracks

The feet of the axis deer are similar to those of other deer of the same size range. The hoofs are hard and black on the outside but tough and rubbery on the ventral surface. Hoofs of the front feet are slightly longer than those of the hind feet, and measure from 4·1 to 6·1 cm. in length along the bottom surface. The outer toe on both front and hind feet is usually slightly longer than the inner one, and all toes taper to a fairly sharp point. Two dew-claws are present above and to the rear of the hoofs on each foot.

The front feet of a number of bucks and does were measured with the idea of comparing them to see if it would be possible to differentiate between the tracks of bucks and does by track size. Both length and width of the hoofs were measured, and the data thus obtained were examined graphically and statistically. The analysis showed that there was no real difference between the size of the hoofs—and hence the tracks—of the sexes. The tracks of a large buck may be told from those of a doe with some chance of correctness if the depth of the track (determined by the weight of the animal) and the placement of the feet can be noted, but not by size alone. The judgment of the factors that go into the making of a track on the ground—the weight of the animal, the hardness of the soil, the speed of movement, the age of the track, etc.—all require such continuous experience that a sportsman of today has little opportunity to acquire the skill of real tracking.

Deformed hoofs appear to be common on the deer living in the rain forest of Molokai where the soil is soft and wet almost continuously, and where there are few rocks in the ground to wear them down. In hooved animals, the outer shell of the hoof grows continuously and is kept worn down by normal abrasion against the soil. Unless driven to it, wild animals seldom wear their hoofs down too much. Horses, however, under domestic use commonly show this type of abuse if worked on hard and rocky soil without shoes. On the other hand, the deer and goats of the wet forest simply do not get enough wear to keep their hoofs worn to normal shape and size.

Goats appear to have more trouble in this respect than deer. This is apparently due to the fact that goat's feet are normally adapted to rocky, mountainous, cliff country, and probably have a faster growth rate. Perhaps they are also harder, and require more wear to keep them in shape. Deer hoofs in the wet areas showed the abnormal growth, but the edges seemed to break off in irregular pieces sooner, indicating that the horn shell is not as tough as, or perhaps is more brittle than, that of goats.

Deer range in some areas overlaps that of feral goats not only on Molokai but also on Lanai, and the tracks of both will be found together. The tracks of the Mouflon sheep (*Ovis musimon*) and the North American pronghorn antelope (*Antilocapra americana*) will also be found in the deer range on Lanai. The goat tracks are usually much more blocky in appearance than those of the deer, being wider and blunter, and giving the impression of a square shape rather than a heart shape, and clear impressions may be readily distinguished from those of deer. However, the hunter must ever be alert to exceptions. On Molokai, particularly in the wet forest areas, tracks were often noted that were very much like those of deer in size and shape, especially the smaller tracks.

Mouflon tracks are slightly blunter than those of the deer and show a somewhat concave outer edge, but the difference is usually apparent only in very clear impressions. Antelope tracks are even more difficult to differentiate from deer tracks, but may appear sharper at the tip of the toe, and may appear more wedge-shaped than those of deer, whose toes have a more convex outer curve and a concave inner curve. There are many variations and exceptions to all these characteristics, associated with many varied conditions.

Voice

One of the most noticeable and interesting characteristics of the axis deer is its voice. It is one of the most vocal of all deer, being rivalled by only a few other Asiatic deer.

There are several fairly well-defined calls uttered by these animals.

The most commonly heard is the ' bark ' of alarm or curiosity, which is a loud, high-pitched ' *Yowp* ! ' that is usually repeated several times. A group of deer seeing something that puzzles or worries them will frequently ' bark ' at it for several minutes or longer while watching intently. After their curiosity has become satisfied, the calling is discontinued. It is used more commonly by does and fawns than by adult bucks, although the latter do ' bark ' when sufficiently aroused by curiosity.

This ' barking ' has been heard over a mile away in the high canyons of the Molokai rain forests, even over the soft noise of drizzling rain ; and on windless days in the dry lowlands, it has been heard from observed deer that were a full mile and a half away.

Besides the common curiosity or ' attention ' bark, there is a short explosive yelp of extreme fright or alarm. This is a short ' *Y-owp* ! ' or ' *Yup* ! ' and is the ultimate in danger signals which all deer within hearing never fail to heed. If a group of deer is suddenly startled and badly frightened, the first one spotting the danger will give this warning yelp, whereupon the whole group, whether or not they too have observed the danger, will take immediate flight without calling. Both bucks and does use these calls, though the calls of the large bucks are slightly hoarser and seem to have a bit more power behind them.

An interesting, and somewhat comical, sidelight to these calls is that the tail gives a spasmodic up-and-down jerk with each ' *Yowp* ! '. It almost appears as if some invisible hand is cranking out the ' *yowps* ' by pumping the tail !

Another call appears to be characteristic only of adult bucks during the rut. Lydekker (1901) describes it as a ' peculiar moaning sort of bellow '. To us it sounds like a low, hoarse modification of the normal call, and may be perhaps described as sounding like ' *yo-o-o-w-w* ', or ' *h-h-a-o-u-u-h* '. It has a low, groaning, forced breathlessness about it that is most difficult to describe, and sounds as though it was being uttered with the last available breath left in the lungs. These calls can be heard at any time of the day, but most often in the morning or evening or at night. Most of them seem to be repeated at intervals of 15 to 20 minutes, though some have been heard to call at intervals of five minutes for a period of some fifteen minutes. The call is not loud, but on quiet days is still easily heard at half a mile. It is an impressive and weird sound and, in the strange world of giant tree ferns and swirling mists of the cloud forest, it is a sound that will long be remembered.

The call appears to be a mating call or, more likely, a call signifying territorial occupation, for bucks with identifiable voices have been heard to call for days from the same spot. A large buck with a herd of does was heard to give this call throughout the mid-afternoon, alternating it with an antler thrashing of kiawe boughs. In the heat of passion the call becomes a moaning roar and, during the excitement of a fight or shoving

contest, bucks often give vent to their rage with a high-pitched, nasal squeal, somewhat like the '*meow*' of an excited house cat.

Young fawns also have several calls with which they summon their mothers. The most common is a high-pitched, nasal '*naya-a-ah* !' similar to the squeal of the bucks, and has a kitten-like sound. Another call begins with a high-pitched, rising whine, and breaks suddenly into a loud raucous squall: '*ee-ee-p-Y-A-AH* !'. Fawns will of course squeal or scream shrilly in fright when caught by predators, or when in pain. Adult deer also will squeal with fright when pulled down by predators or when handled in live trapping, though in the latter case they are not being hurt. Wounded deer have not been heard to utter a sound.

Teeth

The dentition of adult axis deer strongly resembles that of the black-tail deer but can easily be distinguished from it by the two middle incisors, which are very wide and shovel-shaped, with the crowns wider than they are high.

In the lower jaw there are 3 pairs of incisors, one pair of canines (these appear as the outermost incisors), three pairs of pre-molars and three pairs of molars — ten pairs in all. The upper jaw contains no incisors, and in deer a year or more old, no canines. There are three pre-molars and three molars which correspond to their counterparts below. The formula for the axis dentition is:

$$\text{i. } \frac{0-0}{3-3},\ \text{c. } \frac{0-0}{1-1},\ \text{pm. } \frac{3-3}{3-3},\ \text{m. } \frac{3-3}{3-3} = 32.$$

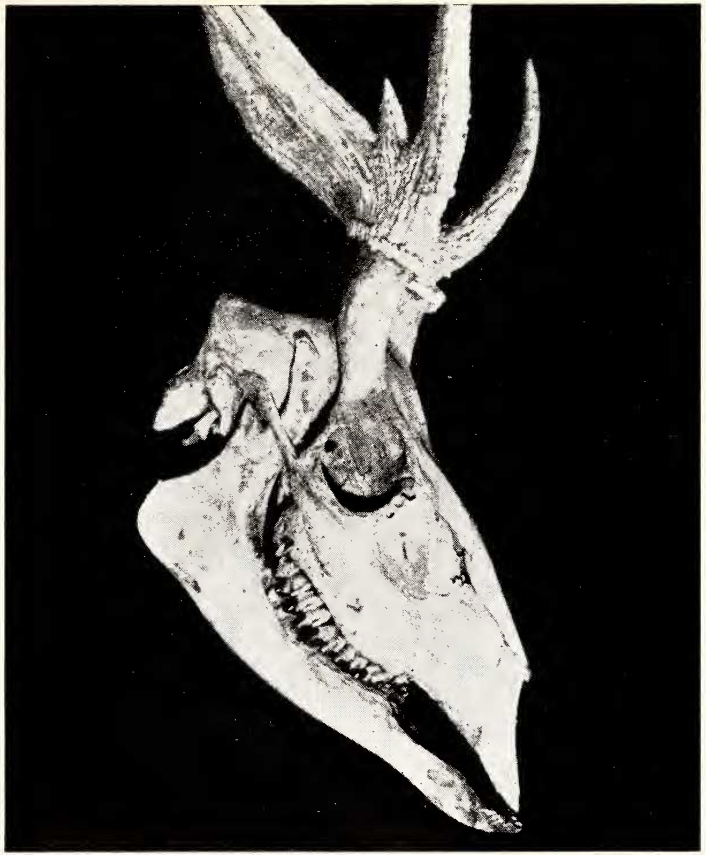
In fawns there is a distinct upper canine tooth on each side, located about midway in the gap between the incisors and first pre-molar. A great deal of controversy has existed over these canines, and whether they are or are not present. Pocock (1943) disclaims their presence, simply because :

> 'They are entirely absent, however, in all the numerous skulls examined in the British Museum.'

This, at least, serves one purpose—to point out the inadequate age distribution of the collection. Fooks (1945) merely adds to the confusion and misinformation by stating :

> 'With reference to Mr. Nolthenius's note on the canine teeth in chital stags (Vol. 45, No. 1, p. 83), I should like to say that after examining a number of chital and sambar for their "tushes" I have only found them in a very rudimentary form and then only in older beasts.'

Fooks's involvement of the sambar as well as his reference to older beasts indicates that he has not examined enough age classes and is confused on the whole subject. Nolthenius (1944) apparently comes closer



Skulls of Axis Deer

Left : Skull of adult buck. *Right :* Skull of fawn, approximately 7 weeks old

In skull of fawn note the well imbedded canine tooth and the absence of canine teeth in the skull of the buck. These teeth, present in all fawns, are shed by the time the animal is one year old and the socket closes, leaving no trace of the former canine teeth. The extra tine above the brow tine in the buck skull is atypical.

(*Photos : Lyman Nichols*)

to the problem, at least in terms of the exception rather than the rule. He says :

> ' No doubt these teeth as found in axis, can only be called rudimentary, they are not solid and fully developed as in the stags of Europe. As a rule they are just under the skin of the upper gums and have not broken through. In a few cases they are visible as small white spots.'
>
> ' They can be lifted out quite easily and rather resemble the thin broken shell of a tiny egg. It is not surprising that the skulls in the British Museum should not show any of these teeth as they are lost at once when the flesh has rotted or the skull has been boiled and cleaned. There is no socket.'

The solution is quite simple. The canines are present in new-born fawns, actually already being present before birth. These canine teeth appear as slim, curved tusks, about one-quarter to one-third of an inch in length. The tooth is imbedded quite firmly at this stage in a very *definite socket.* We have found one skull on Molokai from a fawn so young that the skull bones fell apart, yet the canines were firmly in place in the tiny upper maxilla. There is indeed a socket, and these teeth do not readily fall out when the flesh rots away.

The teeth are quite firmly placed in sockets in young fawns, but gradually loosen as the fawn grows older and usually fall out before the fawn is a year old. Most of them probably are shed by the time the fawn is eight months old. After shedding these teeth, the sockets close up and so are not seen in the adult deer. Occasionally, one or both of these tiny 'tusks ' may be retained by the cartilage of the upper jaw after having come loose from their bone sockets, and are thus found in the gums of the older deer.

Aging Deer

The problem of aging animals by their teeth is not easy, and the determination of the factors by which this can be done is even more difficult in a study of this kind. One needs at least one or two skulls of known age from the various age classes, starting with young fawns and ranging through all adult years. Rarely is this possible. We have only one skull of known age, a 12-month-old buck plus some information on the development from a live deer up to 18 months. Our age determination is based on the order of appearance and approximate time of development judged from the known-age deer.

Temporary premolars are fully present by the time a fawn is a few months old. They can be distinguished by the size and form of the third premolar, which is long and flat crowned but with three distinct cusps or crown areas. Viewed from the outside it appears to have three pillar-like ridges on its side. The first two premolars are shorter and smaller. The permanent molars are added one at a time in the

PLATE XI

Lower Jaws of Axis Deer

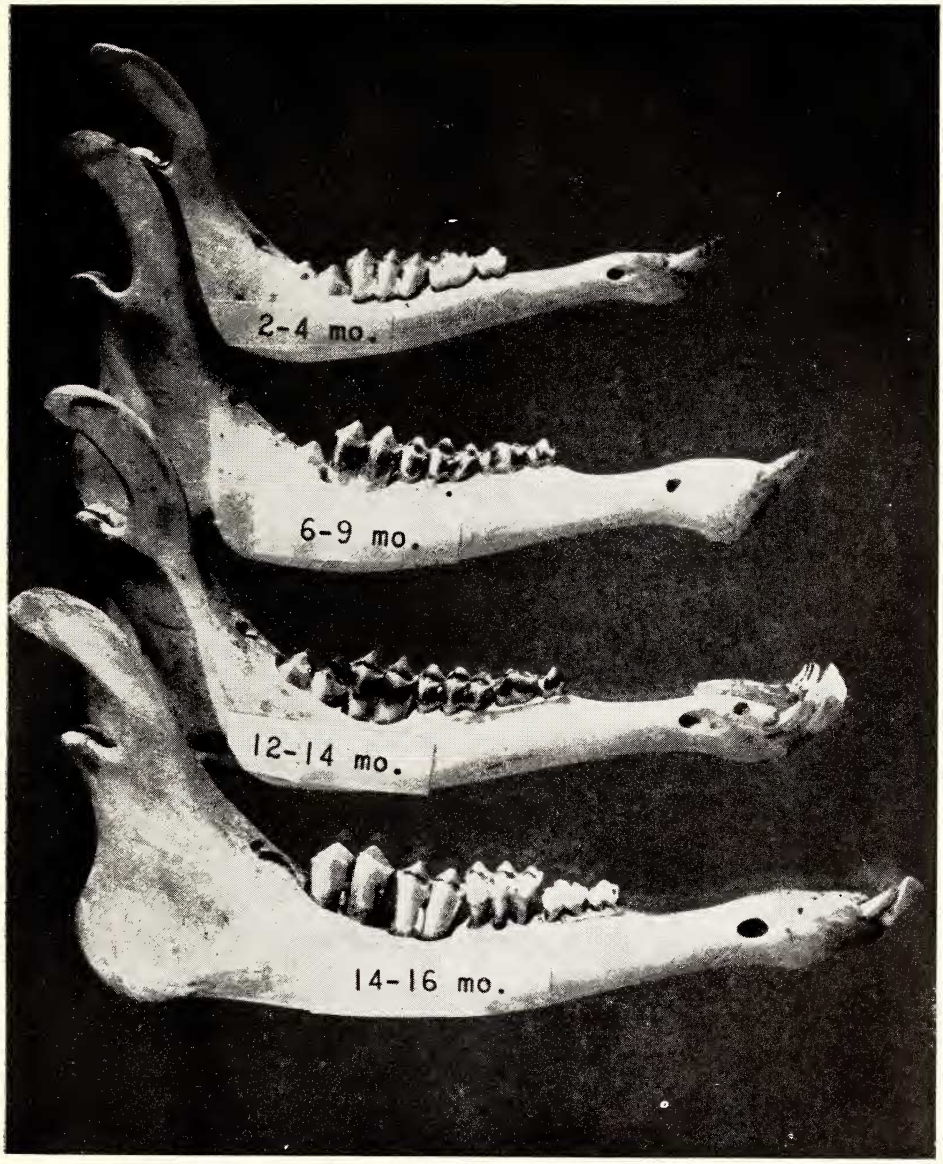
2-4 months — The first molar is just beginning to show at this age. The milk-premolars or temporary premolars are all high-crowned with sharp distinct cusp points. The three-crowned 3rd premolar is distinctive up to about the 18th or 19th month when it is shed. The middle or first pair of incisors are about $\frac{3}{8}$ inch wide at the top. The other incisors are about $\frac{1}{16}$ inch wide. Permanent incisors are about twice these widths. Because the middle incisors are much wider at the top than the base, the crown width will decrease with wear.

6-9 months — The first molar is now fully out and the second molar is just beginning to show. The milk premolars are now beginning to show some wear, particularly the 3rd premolar. The middle incisor also may show some wear and may be narrower at the top than in younger deer.

12-14 months — The middle or first permanent incisor is now in place. The width of this permanent incisor is about $\frac{1}{2}$ inch across the crown. The 2nd molar is about half out and the socket of the 3rd molar is now visible as a wide slit in the angle of the jaw behind the 2nd molar. The premolars are now showing considerable wear.

14-16 months — The 2nd and 3rd temporary incisors and the incisiform canines are still present but show considerable wear. The 2nd molar is now fully out. The 3rd molar is still indicated only by the oval slit in the bone behind the 2nd molar. This opening is however, much wider and has advanced forward in the angle of the jawbone. Note particularly the angle and shape of the front part of the jawbone just behind the incisors. This is due to the permanent incisors imbedded in the bone beneath the temporary incisors. When these permanent teeth are all in place the space occupied by them will close up gradually and the jawbone will flatten out and take on the thin flattened shape of deer two years or older. Note also that the third temporary premolar is being lifted by its permanent replacement.

Graf : Axis Deer



Lower Jaws of Axis Deer

For explanation see page opposite

(*Photo : William Graf*)

order of 1, 2, and 3, starting from the front. Determining age is done by using the presence or absence of certain teeth and the degree of development of the various molars, and then finally by the degree of wear of the various teeth.

Hunters, as well as game managers, should be interested in the age of deer they shoot, and the following outline in combination with the illustrations (Plates XI, XII and XIII) will help a great deal in obtaining some estimate of the age of deer. It is admitted that our outline is purely an estimate beyond about 30 to 36 months. It should be pointed out that the wear of teeth may vary because of variable factors. For example, a deer from the dry, coastal area, with little rain, high wind, and consequently much dust and grit blown on the vegetation, will show much greater wear than a deer of the age from the high, wet mountain forests of Molokai, where the vegetation is virtually dustless and is constantly washed clean by daily rains. Replacement ages will be the same within their limits of variability in these two areas. A deer of 30-36 months age with a virtually complete new set of permanent teeth will look much the same from both areas. However, after this the wear can be expected to be much faster in the dry-land deer than in the forest deer of the wet uplands.

Records from the captive buck ' Willie ' show that the middle pair of deciduous incisors were shed the 63rd week of age and replaced eight days later ; the 2nd pair were shed the 65th and 68th week and fully replaced by the 73rd week. No further records were possible after that, but probably all incisors are replaced by the age of 2 years. This information is useful in conjunction with data given for the molar teeth, though most people would have difficulty in determining what is a temporary and what is a permanent incisor.

Age criteria in the illustrations (Plates XI, XII, and XIII) are fairly close up to 36 months. Above four years the aging becomes a matter of judgment and comparison with known-age skulls which we lack today.

Other Ungulate Skulls

Hunters may at times find the skulls of other ungulates, such as goats, mouflon sheep, or pronghorn antelope, in the field on Lanai and Molokai. These are for the most part easily separated from the axis deer. The skull of a buck deer obviously will show at least antler pedicles, the bony, flat-topped, peg-like protrusions rising about 1 to $1\frac{1}{2}$ inches above the surface of the frontal bones. Antlers, of course, easily identify the skull from any other ungulate. On Kauai, where the North American blacktail deer (*Odocoileus hemionus*) has been introduced, this will be the only deer skull to be found, and pedicles are much lower

PLATE XII

Lower Jaws of Axis Deer

18-24 months — All incisors are in by the end of this age-class. The replacement of the 2nd incisor is probably by 18 to 20 months (see text) and the 3rd incisor and incisiform canines between 20 and 24 months. The 2nd and 3rd temporary premolars are in the process of replacement. In the upper specimen (female) the replacement is not as advanced as in the lower specimen (male). The permanent premolar is just visible beneath the three-crowned temporary 3rd premolar in the upper specimen and also beneath the 2nd temporary premolar in the 2nd specimen. In this specimen the 3rd molar is also farther out than in the upper one. There may be a difference in the ages of tooth replacement in sexes. Note the flattening of the mandible behind the incisors as the permanent incisors push out and replace the milk incisors.

30-36 months — All permanent teeth are now present. Note the difference between the permanent and temporary pre-molars, particularly the 3rd pre-molar, which no longer has three cusps. The crowns are all high and the points of the cusps are sharp triangles. The anterior part of the mandible behind the incisors is losing more of the thickened shape of the temporary tooth condition.

4-5 years — Similar to preceding condition. Crowns are still high and the cusps still angular but the points are now rounded off and teeth are definitely showing wear, particularly on the outer side. Note the difference in the appearance of the 1st molar and the 3rd and 2nd premolar. The greatest wear is on the 1st molar and the 3rd premolar.

Graf : Axis Deer

Lower Jaws of Axis Deer

For explanation see page opposite

(*Photo : William Graf*)

than in the axis deer. Also, antlers are readily distinguished. In doe skulls the two middle incisors, with their wide shovel shape, will easily distinguish the axis deer from the blacktail. The males of other ungulates that are found in the area all have true horns ; that is, a bony core rising from the frontal bones, covered with a horny sheath, as in goats, sheep, and antelope. If the horn is missing the bony core will be there, rounded and back-curving in sheep and goats, and straight and flattened at the upper end in the antelope. Most female goats will show this horn core, but smaller. Female deer, female mouflon, and most female antelope have no horn distinction. However, the female mouflon skulls are easily distinguished from doe deer skulls by their general shape. The mouflon skulls are shorter and broader, with a distinct concave or dished outline, while doe skulls are long and narrow with a fairly straight outline from forehead to nose. Doe antelope skulls are similar in general appearance to doe deer skulls, but have very large, heavy eye sockets (indicating their dependence on vision and high eye development) located more to rear—giving them a greater field of vision to side and rear. Antelope also have middle incisors which are narrower than they are long, in contrast to the very wide spatulate middle incisors of the axis deer. Photographs should be carefully examined for other distinctive features.

Faecal Pellets

The fæcal pellets of axis deer assume many shapes typical of other deer, sheep, goats, and antelope, and it would be very difficult to state with certainty that a certain pellet group was that of a deer. The pellets may range in size from one-quarter to three-eighth of an inch in diameter and from one-half to one inch in length, and be deposited separately in a group, or in a solid mass. They often are tear-drop shaped with a dimple in the large end and several indentations on the sides, or else in the shape of cylinders with rounded ends, but may take many forms. They are dark green and soft when fresh, but become dark brown or black and hard with drying.

Goat pellets seldom have the tear-drop shape, and are usually blunt, rounded cylinders, while mouflon pellets are more typically tear-drop in appearance, but less than one-half inch in length. However, the pellets of each species are so variable, that they cannot be definitely identified in all cases by pellet shape alone.

The defæcation rate of one captive buck on a diet of natural food was measured for a period of four days to determine the average number of pellet groups deposited per day. The rate in this case was found to be about 15·5 groups per day.

PLATE XIII

Lower Jaws of Axis Deer

5-6 years — The points of the cusps are showing much wear and are dulled or ground down. The condition of the incisors should be noted. The middle and outer incisors will be still about the same length and the middle incisor is still almost full width. Top specimen shows the first molar partly broken away and other teeth show heavy chipping of the points of the cusps. This animal apparently came in contact with hard, gritty food. Such specimens will still show high crowns but chipped rather than worn points. The upper specimen in this case is undoubtedly older, probably at the upper limit of this age class, whereas the second specimen shown is at the lower limit of its age class.

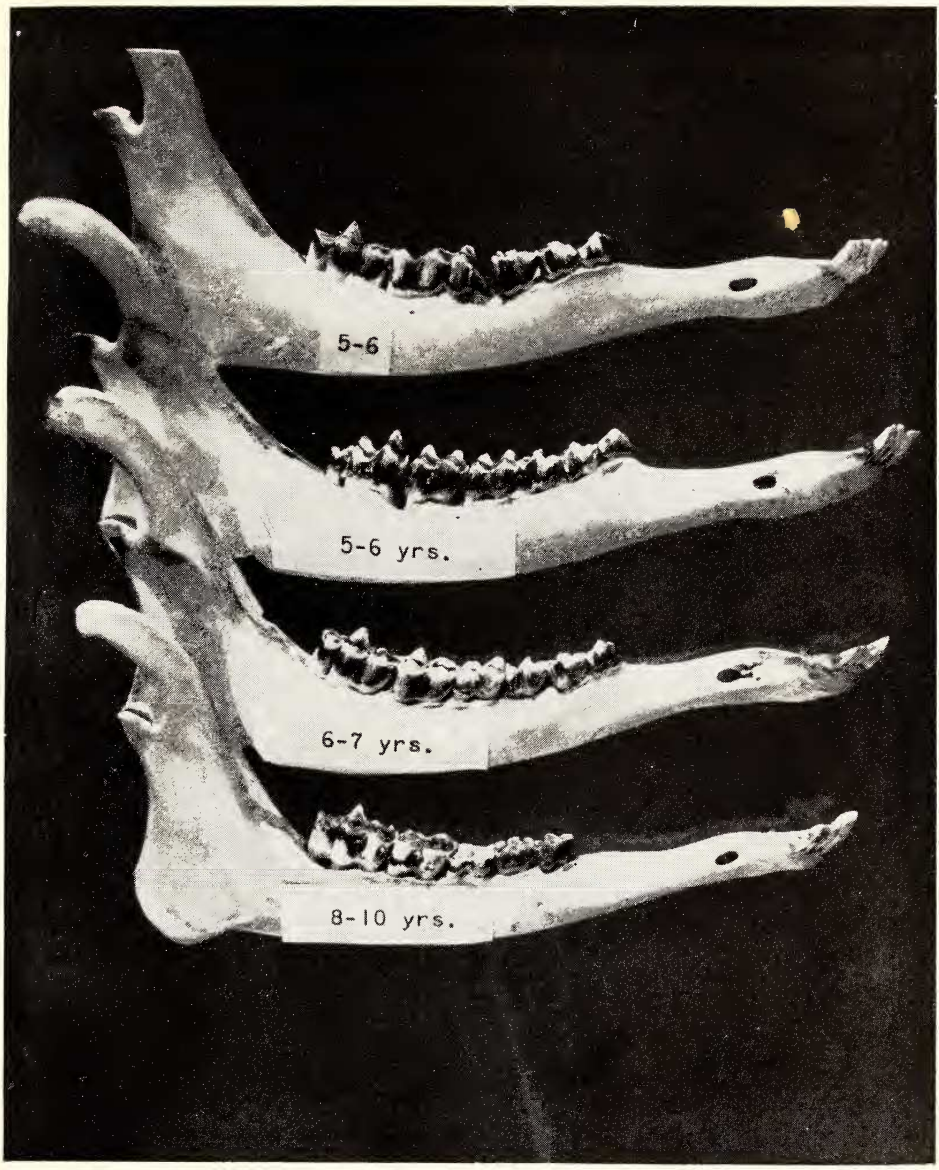
6-7 years — The crowns of all teeth are now well flattened and definitely nearer the gum line. Crowns are reduced about $\frac{1}{3}$ to $\frac{1}{2}$ of their original height and have a fairly flattened appearance. Some evidence of the original triangular pointed cusps is still evident. The first premolar still shows a triangular shape. The incisors show shortening with wear and the outer ones are shorter now than the 1st or middle pair.

8-10 years — All the teeth are now badly worn. The 1st molar is now almost down to the gum-line and presents a concave or cup shape, and even the first premolar is now square topped. The incisors are much worn and the middle incisor in this age-class as in the preceding one will be no wider at the top than in a 9 month old deer. The outer incisors are usually much shorter than the 1st pair of incisors.

Note that the last age-class specimen has only five molariform teeth. The first premolar is lacking. In some specimens the 3rd premolar was missing, a condition that apparently is not uncommon.

All age-classes above 24 months are estimates and ages above 4 years are particularly difficult to judge under variable forage conditions. The examples listed are an average guide to follow but their age may vary depending on conditions.

Graf : Axis Deer



Lower Jaws of Axis Deer

For explanation see page opposite.

(*Photo : William Graf*)

Temperature

The temperatures of four freshly-killed adult deer were taken rectally. These were found to be 101·5, 101·6, 101·2, and 101·2 degrees F. Normal temperature is probably about 101·3 to 101·4. These deer were at rest and were killed instantly. A large buck that had run a short distance was shot but lived about 10 minutes before dying. The temperature taken rectally about 45 minutes after death was 102·7 degrees F.

Senses

All senses are very highly developed in the axis deer. Probably the sense of smell is the most important, but certainly hearing is not far behind in use and importance ; in fact, it is probably equally important, depending on circumstances and conditions. It should be kept in mind by the reader that senses are developed in proportion to the usefulness to the animal. There is too much tendency on the part of sportsmen and popular writers to make hard and fast rules on the basis of general observations.

Both deer and antelope have been observed (Graf 1956) that disregarded their sense of smell, and depended either on eyesight and/or hearing entirely. Under these conditions it was possible to approach to within a few yards with the wind at the observer's back without causing the animal any alarm. Yet in all these cases the animals showed extremely keen alertness to sight and sound.

In deer, normally a forest animal, vision is often greatly restricted and consequently is of little use. Scent and sound are of great importance, and are constantly used. An animal from a dense forest country may at times appear almost blind in its inability to spot an enemy even in the open. Or it may appear quite stupid and remain standing, staring at a man apparently without recognizing him. The answer is quite simply that without scent or sound, by which the animal normally recognizes its enemy, there is no sight recognition of an enemy which the animal may never have seen before. In short, it is unfamiliarity, through a sense by means of which it does not recognize danger, that causes the apparently stupid and unorthodox behaviour of an animal.

In our experience, the senses of smell, sight, and hearing are extremely good in the axis deer. These deer can scent danger that is almost a mile away up-wind from them. They seem to locate food primarily by scent, and it may be that these deer (and perhaps others) are far-sighted, a condition that would not be too strange since the greatest need is to see keenly at a distance. Eyesight at close range, that is, a few feet away, appears to be poor. Beyond a few yards it is excellent. There

is another explanation for this. The captive buck had difficulty in locating food by sight that was in plain view a few inches from his nose. Actually this should not be considered strange since the placement of the eyes—far to the side of the head—is not conducive to locating objects directly under the nose. Eyes so placed are strictly for detecting danger at a distance, not for critical viewing at short range. Critical focus for the purpose of food gathering is of little use to an animal that feeds on the type of food, and in the manner of a deer, and it is quite possible that ungulates' eyes do not focus sharply at very short distances.

Whether deer are colour blind or not, we are unprepared to say. Their eyes are excellent and they can often recognize a man at considerable distance even though he is standing still. This is particularly true on the west end of Molokai where hunting has conditioned the deer to the use of their eyes more than elsewhere. On the east end of Molokai in the high, wet forest, deer showed the typical sight-response of animals not used to using their eyes—as was to be expected in the heavy jungle country and where man is seldom encountered by them.

Hearing is extremely acute, and the ability of the animals to distinguish danger signals from ordinary sounds is at times amazing. Here again it is a matter of conditioning and training. The Molokai west-end deer showed the highest degree of conditioning, the east-end forest deer the poorest.

Gaits

When feeding, the axis deer usually moves along at a slow walk, but it may walk rapidly at times, and occasionally breaks into a trot. When frightened, however, they run with a speed and agility that is surprising. Their run is a low, stretched-out, well co-ordinated flow of motion, with the footwork of a greyhound at full speed, and they can negotiate rocky ground and brush with flashing ease. We have clocked them at 50 miles per hour from a helicopter, but that was ' air-speed ', and the true ground-speed could have been somewhat lower due to head winds. A few observations on Molokai, when deer angled across in front of a jeep racing to intercept them, indicated that they are able to push their speed up to 40 miles per hour for short bursts. However, they tire easily and do not appear able to keep up top speed for long distances, soon dropping back into a slow gallop, then a trot, and finally a walk when pursued steadily, eventually seeking cover in which to hide and rest. This accounts for the ease with which Molokai Ranch cowboys were able to lasso them for the original shipment to Lanai ; they chased them on horseback in relays until the deer slowed enough so that they could catch them.

Leaps of 15 to 18 feet have been recorded for deer in full panic-stricken flight, but these are ' broad-jumps ' not ' high-jumps '. In the

wild, they do not usually jump over obstacles, but prefer to run around them. Captive deer, on the other hand, can soon learn to make high-jumps when necessary, and have been observed to clear a six-foot fence easily from a standing start. Even tiny fawns can bounce over a surprisingly tall barrier. Wild deer, without reason for learning or need to do so, would fail to take even a five-foot fence, preferring nearly always to slip through or under it.

HABITS AND BEHAVIOUR

Normal and Abnormal Behaviour Judgment

In general the behaviour and habits of the axis deer show its relationship to other members of the genus *Cervus* as a whole. However, in many specific details it varies not only from this pattern but varies to a considerable degree in specific habits between each of the islands on which it is found in Hawaii.

Such specific variations are due to the conditions brought on by climate and weather, terrain, and food which may force the animal to adopt behaviour habits that differ from the normal. When abnormal pressure factors are brought to bear upon the animals, one can expect to observe patterns of behaviour that are radically different from the normal. Conversely, when radically different or unusual behaviour is observed, one should look closely to see the cause for such behaviour.

The problem is then to determine what ' normal conditions ' are and what is ' normal behaviour '.

The inexperienced observer, scientist as well as layman, all too often judges by anthropomorphic standards. It is most difficult to avoid doing this, especially when we have nothing else to judge by except our own experiences. This, of course, is wrong. Deer behaviour, or any other animal behaviour, must be judged by its own standards—deer, by deer standards in general, and most specifically by the kind of deer under consideration.

The problem is in knowing what constitutes *normal conditions,* and *normal behaviour.* If we know what normal conditions are, we can come closer to deciding what normal behaviour is. If we do not know this, then we can only accept the behaviour as an expression of the conditions. Also, if the abnormal or unusual conditions persist as a constant situation, then the behaviour must be considered as normal for the conditions. The important point to remember is that varying conditions may create varying habits and that, while many behaviour characteristics are inborn, others can be acquired or varied.

Generally speaking, there is a feeding, herding, breeding, etc. pattern which resembles that common or related to other cervids. Also, in

general the axis deer in India and Hawaii have certain habits in common, but in some respects the axis deer of Hawaii appear to differ not only from their Indian relatives, but show varying habits between the island groups.

It takes a great deal of time in the field observing both habitat and habits to determine what is normal and what is not normal habitat or normal behaviour. Hunters, who spend only a few days a year afield, should keep this in mind. It will help prevent many false assumptions and conclusions and the establishment of so many commonly held dogmas which one finds firmly fixed in the minds of laymen and hunters.

With this in mind let us take a look at the behaviour and habits of deer in Hawaii.

On the whole, there is a degree of gregariousness similar to that in elk and other deer, but not as well developed as in the most specialized groups. They like to be in each other's company, but form only loose aggregations or herds. Feeding is usually during the early and late hours, with regular movements to water during the hot parts of the year. They graze when grass is green and abundant, and browse when grass is scarce, or when browse is particularly palatable or abundant. Groups or herds are matriarchal in nature—i.e. old does generally are the leaders, never bucks. There is evidence of nursery formation among fawns, and there is a well-defined 'signpost' behaviourism in bucks. All these are characteristic of deer in general, but all have their own variations and specific characteristics within or around these basic patterns.

Even as a new-born fawn, the axis deer exhibits characteristics not common to others and which seem to reflect certain adult characteristics to be discussed later. Normally, a new-born fawn shows no fear of man and may be readily approached and even handled. This does not appear to be the case with axis fawns. Those which were encountered, so young that they could only wobble about on rubbery legs, promptly showed every sign of fear and recognition of an enemy, and made every attempt, and quite successfully too, to flee.

Temperament and Alertness

Axis deer, particularly the females, are extremely alert and wary. In their nervousness, they are constantly on edge during the daytime, often jumping up and running from imagined dangers, as well as from real ones. They continually test the breeze, pausing to look and listen for signs of danger, and are thus difficult to approach. The older bucks, however appear to be a bit less alert—or, at least, less nervous than the young bucks and does. When with does, they seem to depend to some degree on the alertness of the does for their own protection.

When alone, they are usually somewhat easier to approach than does if care is taken to stalk them up-wind—the least trace of human scent will put any of them to flight. Young fawns of both sexes, though instinctively alert and nervous, sometimes get carried away by their playing, curiosity, or feeding, and at such times are not as sensitive to the approach of danger as their mothers, who are constantly aware of all happenings in their vicinity. During the night, the nervousness is much reduced and the deer appear to be a little less alert than during the day ; even the does may then be approached fairly easily if wind direction is watched.

This inborn wildness seems to be retained even by deer raised in captivity under close proximity to man. The only exception seems to be in those raised by hand and handled constantly, but even these 'tame' deer will instantly become wild and panic-stricken when frightened by unfamiliar stimuli.

At the Honolulu zoo, the well-fed, well-kept small herd of axis deer will promptly retire to the far end of their roomy paddock at the approach of a visitor. They are rarely found near the outer fence as is commonly the case with other species of deer. This negative reaction is not an accident and has been watched too many times to be mistaken. There is a definite nervousness and watchfulness in the herd when visitors stand in front of the paddock. The does and young bucks in the small herd kept by Mr. Noah Pekelo of Molokai, showed the same behaviour pattern. All of these were born and raised in captivity. Yet the approach of even members of the Pekelo family would cause the animals to run to the far side of the pen, and the approach of strangers would create a wild panic, with animals dashing wildly into the wire fencing of their pen. Only the old buck, Rudolph, raised indoors on a bottle, showed no fear of men, and in fact was exceedingly pugnacious most of the year except when his antlers were shed or still very young and soft.

There appears to be a greater degree of nervousness and wildness demonstrated among wild deer on the Molokai Ranch range than elsewhere. This undoubtedly is due to the extremely heavy hunting that goes on the year round, as well as the type of hunting that goes on in this area, and not in other areas.

This inborn wildness and timidity may also be the reason for this deer's demand for overstorey cover, such as a forest cover. It apparently derives some feeling of security from the partial concealment and shading, yet dislikes the close confinement of dense and continuous cover—there must always be openings or clearings near by, or an open parkland forest.

On Molokai Ranch this affinity for cover was developed and dis-

played perhaps to the highest degree. A typical example that could be observed almost any evening is the following :

A herd of 15 to 20 deer, made up of does, fawns, and perhaps several young bucks and an old mature buck, ventures out of a thicket of kiawes to feed at the edge of an open pasture at the start of their evening's foraging. As they feed out into the clearing, there is the usual pause and quick look up and around for any possible danger. Gradually, as the distance from the forest increases, the frequency with which heads are thrown up increases, there is a gradual but definite build-up in the tenseness and alertness with which the animals move. This changes to outright nervousness as the distance widens to 300 yards or more and, finally, as the distance from cover increases still more, the nervousness reaches a point where there is very little grazing but more looking about and nervous stepping around. This reaches the point where, finally, an animal makes a nervous jump, or jostles another one, which may result in another nervous jump, a startled yelp, and the whole herd breaks into a wild, helter-skelter flight back towards the forest edge.

The speed and panic is high, yet it shows a direct relationship to the origin of the cause for the panic, namely the distance from shelter. As the distance from the forest decreases, so does the panic. The wild racing slows to an easy run, then a trot, and finally to a walk, and comes to a halt near the edge of the forest. Here the group stands around with a bewildered and puzzled look about it that needs only someone to say : ' who started that ? what happened ? ' The animals walk back and forth, peer here and there ; perhaps one gives voice to a shrill ' *ye-e-o-op* ', which may be taken up by another one and is continued back and forth for minutes without anyone really believing anyone else—for these are not really alarm calls which, when uttered lower and sharper, leave no room for doubt in anyone's mind.

Such self-generated flights have been observed many times on Molokai Ranch, where this type of behaviour seems to be most common. One is reminded of a group of young schoolboys out on a ghost hunt to the local cemetery or haunted house—the closer they come to the object, or perhaps the farther from the known security of their car, the more nervous or fidgety they become, until some imagined or misinterpreted sight or sound sets them into flight. There is no doubt that the objectives and minds involved are quite different, but the psychological causes that create the condition and trigger the reaction are the same in both cases.

Another behaviourism that is closely related is one that often occurs in or near open forests, where the deer do not ever get far enough away from surrounding cover to display the spontaneous panic reaction, but which is open enough to make them thoroughly alert. This extra alertness is always manifest whenever they step into a clearing, even a

relatively small one, or thin patchy forest. Under such conditions, either as a result of a real but passing danger or of an imagined one, a deer gives its high pitched alarm bark. This call is clear and distinct and longer than the real alarm call, and might better be termed the 'alert' call. It may evoke a short run which stops after a few half-hearted bounds. After this first moment of alarm, the group stands peering in the direction of the supposed danger. The alarm-giver repeats the call and others, without really knowing what it is all about, may also call. This may go on for several minutes until the whole herd loses its tense attitude. Individuals may wander about in a relaxed and indifferent attitude, now and then throwing up their heads to give a yelp, others answering, until there may be a sort of chain reaction of yelping calls repeated with considerable frequency as the herd wanders about picking at feed or just standing around.

Such a chorus may continue for a considerable period of time following the incident which initiated it and which is always something which has no immediate real threat to the herd. It can be a cow that shows up on the horizon a half mile away, a stray and unidentifiable scent that is picked up momentarily, or a sound, or finally just an imagined danger. Such calling, or 'talking', sessions are so common on Molokai that one is hard put to try to explain the comparative silence of the deer on Lanai. The Lanai deer do, of course, call at times. But even genuine alarm calls are less frequent, while 'talking' sessions, such as those described on Molokai, are even rarer.

Here one could be tempted to say: 'Lanai conditions are more nearly normal. The very limited hunting permits the deer to live a relatively undisturbed life and therefore express themselves in a more normal and natural way.' It is a conclusion which can leave one feeling quite smug and self-satisfied at the ease of solution of the problem—until one becomes acquainted with the deer of the cloud forest of east Molokai. These deer are hunted even less than the Lanai deer. In fact some of these deer may never see a man throughout their lives. They live under almost true wilderness conditions. Yet they are as talkative as their relatives some thirty miles away on the opposite end of the island. Small groups have been observed on distant ridges a half mile or more away, some feeding, some resting, yet now and then at fairly regular intervals one of them, usually an older doe, utters her sharp, clear yelp.

Such calling was a real boon to us while working in the rain forest, both in helping to locate deer for collecting purposes and for observation.

Daily Movements

Phillips (1935) says of the axis deer of Ceylon: 'Except where they have been much shot at and harried they are diurnally inclined and feed in the mornings and evenings ; resting during the heat of the day in the shade of the jungle.' Prater (1935) concurs in this. He says : ' They are less nocturnal than sambar and feed till late in the morning and again in the afternoon, and lie down in the interval in some shaded spot.'

These statements are generally true of the Hawaiian axis deer also. The heat probably influences them more than daylight or darkness. On Molokai during the cool winter months deer could be seen active until mid-morning or even later. With the hotter weather, activity would cease earlier and start later in the afternoon. However even here there were exceptions, and in the protection of the open kiawe forest of the leeward west end, where there was little human activity, deer were often seen feeding and active as late as 10 and 11 a.m. or as early as 2 and 3 p.m. Such activity is, of course, dictated largely by how well-fed and satisfied the animal is. Once the stomach is filled, there is little incentive to move about, and the animal usually lies down to chew its cud and rest.

In this part of the range below Mauna Loa, many of the water troughs—the sole source of water—were well above the kiawe forest, some as much as a half-mile above the main fringe of the forest. Deer began to show up at the edge of the forest just before sunset, occasionally as much as an hour before sunset if the weather was relatively cool. They loitered just within or at the edge of the cover, gradually working farther out as the light fades. None were observed to go to these troughs before it was too dark to see. They gradually wandered uphill to water during the night, feeding, drinking, and then returning to the forest by sun-up. At the first hint of dawn the deer would be heading back to cover. Again, the farther away from the forest, the more hurried the pace, often a trot or even a lope. As they neared the forest, the pace would slow to a leisurely walk, and finally there would again be a period of loafing near the edge of the trees, perhaps some feeding, and at last retirement into cover by 7 a.m. to 8 a.m. at the latest. This retirement from the edge of the forest did not, however, stop all activities. If followed up into the forest, some deer could be found grazing or browsing as late as 9 or 10 a.m.

In Papahaku Forest, a beautiful old-growth kiawe forest that stretches for two miles back of Papahaku beach on the west end of the island, deer were observed active all day during the kiawe-bean season. Beans appeared to reach their peak abundance here in October and November during the study period, and were eagerly sought by the deer. During

the 1957 season, beans were relatively scarce. Food conditions in general were also very poor on the west end, and the forest itself was literally trampled bare by cattle. Only a few hardy lantana shrubs that had reached large size managed to survive under the closed canopy of this forest.

On 5 November 1957, for example, deer were active all day, moving singly and in groups of two to five or six about the forest in search of fallen beans. Cattle and horses also were actively searching for the beans. When a bean dropped within hearing of the deer, they would literally race each other to get to it first. Livestock, particularly the horses, would also respond to the sound of a falling bean, so that competition was high for this food. These beans, like our mesquite beans of the south-west, are high in sugars, with sugar content running up to 25%. The kiawe trees were originally introduced as a supplementary cattle feed. An insect pest that now infects the beans has much reduced the dependability of this crop.

On December 6, a group of 23 deer was observed in the open in a medium-sized forest clearing between 9 and 10 a.m. Generally, however, the Molokai west-end deer cease all activities in the open by 7 to 8 a.m. and do not venture out into the large clearings or fields until 5 p.m. or later.

On the west end, where the water troughs were within the forest and not more than 100 feet from the nearest cover, the deer came regularly in the late afternoons to water. Usually the first individuals would start arriving about 4 p.m., occasionally a few as early as 3 p.m. The main groups and herds would usually drift in after 4 to 5 p.m., always arriving from the side with the best cover. At the main Papahaku trough, they preferred to come in from the east and north-east side which provided good forest cover as well as the shelter of a shallow ravine. This part of the forest is hunted regularly and deer are shot even at the watering place which lies in a clearing some 200 to 250 feet wide.

Deer arrive at the edge of the clearing from the gulch, or north-east side, and spend some time standing and milling around within the edge of the trees. The animals show a great alertness and wariness, not only in general but toward each other. There is a stiff-legged wariness as they mingle ; obviously many are strangers to each other, or at least not regular associates. Drinking is done singly or in small groups. Usually one individual, often a doe, will approach the trough warily, tail raised stiffly ; her gait is measured and halting and as she nears the trough, her neck stretches farther and farther out towards it. By the time she is at the trough she is literally leaning forward, reaching for the edge with her nose. In this way, standing as far back as possible, she drinks ; she may leap back once or twice and re-approach the trough again ; drinking is hurried and often not completed in one operation.

These water troughs swarm with honey bees during the dry season ; many fall in and float or swim about in the water so that not only is the air swarming with hundreds of bees, but often there are almost as many in the water as in the air. This buzzing swarm of bees is no doubt an annoyance to the deer and perhaps a cause of alarm and fear.

After one animal has approached the trough, others become more venturesome, though usually only in small groups. The rest may mill about behind these, stepping warily around each other with stiffly erect tails, like so many strange dogs. Calling may start and may be carried on for a time, simply ' talking ' back and forth, both by animals in the clearing and others coming in.

A most interesting feature of the behaviourism around the watering troughs is the deer's reaction to the fencing, and particularly the gates, around the troughs.

The Papahaku troughs, as well as a number of other troughs on the west end, were situated in a fenced cattle corral. These corrals were usually rectangular or square and about 200 to 300 feet across ; the fence, usually made of smooth strands of wire and wooden posts, presented no problem to the deer. The gates, 15-20 feet wide, were always left open. Such fences and gates made it possible to control the use of water by cattle as well as to corral cattle at the water trough.

It was most interesting to note that deer never used the gates at a number of these fenced water troughs on the west end though these troughs were used daily throughout the dry season by hundreds of deer. In every case deer crawled under or through the fence, no matter how inconvenient, rather than go through the gate. These troughs were checked for tracks on numerous occasions throughout the dry season, and not once were tracks found entering or leaving through the gate. A coincidence ? It is difficult to explain such a coincidence when numerous tracks were to be found going through the fence near the gate, not once but consistently on successive nights.

On Lanai, deer generally remained under cover during the daytime and were rarely seen moving about in the open until just before sunset. An hour or so before sundown they would begin to emerge from their daytime resting places, and would be seen browsing and grazing along the edges of the coverts. There, as on Molokai, they are hesitant and nervous when first leaving their protective cover, but as darkness approaches they become bolder and work farther and farther from the thickets and onto the open ridges and hillsides. Since the best cover there, as on Molokai, is usually along the coast or in the gulch bottoms, the evening drift is predominantly uphill towards the open ridge tops. This is particularly noticeable along the northern coastline where the deer may move uphill two or three miles from the kiawe forests before the night is over, with a climb of perhaps 500 to 1000 feet in elevation.

Where the dense and attractive coastal forest is not present, the deer may spend the day at fairly high elevations wherever cover is available, so that the evening feeding is just on the near-by open ridges rather than up-slope. It is possible that this upward movement may be towards the zone or elevation in which nightly dews fall and thereby provide more moisture in terms of succulence as well as water on the grass.

There is no comparable movement on Molokai except that described for the leeward shore water troughs, which are situated well above the forest line at altitudes up to 1000 feet. East of Mapulehu on Molokai, and still on the leeward side, there is some movement of deer down from the cooler higher elevations into the lowland kiawes where water troughs are located. This is an area where the trade winds and the cooler moisture conditions of the east end make themselves felt. There is a higher open forest in some sections here, and deer prefer to rest and feed at the higher elevations and come down to water at the coastal troughs.

Along the eastern coast of Lanai, at the base of the big ridges leading down from Lanaihale, the evening drift is the reverse of that along the western, northern, and north-eastern coasts. Here many of the deer spend their days in the lower ends of the gulches and move down into the coastal forests in the evening and at night to feed.

Feeding goes on throughout the night, either continuously or intermittently between short periods of rest. They seem to become much more confident after dark, perhaps feeling better protected by the cover of darkness, and are not nearly so prone to take to their heels over disturbances. They calmly feed out onto open slopes that they would not normally set foot on during the day, and where their range adjoins the pineapple fields on Lanai, may wander out onto the dirt roads along the edges of the fields, picking at weeds made succulent by farm irrigation. Occasionally a few work into the cultivated fields for a quarter of a mile or more from the nearest brush along the edge.

On Molokai, there was no activity observed on the roads into or along the edges of the pineapple fields. The difference may be due to a greater reluctance on the part of Molokai deer to leave cover for any distance beyond the maximum 300 to 400 yards, but more probably is due to the combination of fences along the edges of the pineapple fields and the distance below these fences to reasonable forest cover.

As daylight approaches, the deer that have been feeding on the open ridges on Lanai begin to move slowly downward again, feeding as they go, while generally working their way towards the cover of the forest or dense brush in the gulch bottoms. By some two hours after sunrise, there is rarely a deer in sight in the open, though of course some exceptions to this occur and animals may occasionally be observed moving about even at midday. The majority drift into the heavy brush along the inland fringe of coastal kiawe forests or into the dense brush or forest

that lines the sides and bottoms of many of the gulches. Where the coastal forest is not available, they move into such patches of cover as are suitable for protection and shade. As on Molokai, the deer on Lanai continue to browse and graze along after reaching cover, or just dawdle along or stand round doing nothing. When they find a suitable place, they bed down to spend the day, resting and chewing their cud. These periods of rest may be interspersed with short feeding periods. Resting animals rarely remain bedded continuously for a long period of time, but usually get up to stretch, turn around, or move about a little, bedding down again after a half hour or so in the same or a different spot.

Individual deer appear to be fairly regular in their daily feeding rounds if undisturbed, and if the weather remains the same. For example, a small herd occupying the lower fringes of the eucalyptus forest behind Lanai City would move out of the forest regularly each evening along a similar route and spend the night feeding in an abandoned, weed-grown pineapple field, the open hillside, the fields between the town and the forest, or occasionally out on the golf course. In the early morning they would return slowly to the forest where they spent the day. Once their route and timetable was established, they could be found almost at a given time and place with a fair degree of certainty. Deer with distinctive markings in other areas have also been observed to follow roughly the same circuit day after day if undisturbed.

Resting

During the night between periods of feeding, axis deer frequently bed down to rest and chew their cud. Because of their confidence in the protective cover of darkness, they lie down wherever they happen to be without seeking cover. The use of a spotlight at night shows small groups of deer scattered over the hillsides and flats, with some feeding and others lying down, often right out in the open.

In the morning, after they have reached cover, many deer spend some time just loitering under the trees before seeking their day-beds. These loafing areas are usually found within a grove of good-sized kiawe trees surrounded by a screen of smaller growth which protects the interior of the grove from observation. They are marked by well-trampled, and usually, bare ground, buck-rubbed tree trunks and branches, and large amounts of droppings. Some deer lie down in these spots and spend the day resting and picking at what forage is available there, but most soon wander away to search out more favourable bedding sites.

Preferred spots for beds are generally in the shade of kiawe trees, large klu bushes, or wiliwili trees, though some just lie down at the base of a large rock screened by a little shrubbery. On Molokai where there is always an abundance of kiawe cover, it was noted that deer liked to

pick flat benches on the sides of gulches or slopes. In areas where the kiawes are widely spaced, the trees are wide-branching with branches reaching almost to the ground. Such trees provided favourite resting spots, the deer crawling under the low-hanging branches and bedding down on the clear ground underneath. In the rain forest, deer were observed bedded in open pockets on the sides of canyons. Here, however, the grass was so high that a deer lying down was almost invisible.

Beds may be on ridge tops where cover is available, but more often they are on the edges, slopes, and bottoms of the larger gulches, where, if disturbed, the deer can reach other cover in a few leaps, or run down or across the gulch putting it between themselves and the source of danger.

Beds appear to be picked for comfort as well as concealment and safety ; on hot days shaded beds will be used, while on cool days deer will often lie in beds open to the warmth of the sun. The beds are often situated on the lower or down-hill side of a clump of bushes or trees under the rim of a gulch, where there is a good view of the country below.

Since deer, like other ungulates, tend to turn their back to the wind, one might be tempted to conclude that deer pick their beds with a down-wind view in order to be able to see danger in front as well as to scent it approaching from the rear. However, one can find almost as many cases where there is no correlation between the way in which the animal lies and its ability to foresee danger. Sites on the sides of hills or canyon walls generally present a good view downhill, and if the wind happens to be at the animal's back from across the top of the gulch—as it often is on certain parts of the islands where the tradewinds blow across the gulches at an angle—then it might appear that the deer possess a judgment and sagacity which such animals are not likely to have. With a change from the normal tradewinds, the wind and view would often be from the same direction, thus offering no particular advantage of scent to the deer's usual bedding site.

If there is a slight slope to the bed, the deer lies with its head in the direction of the higher part of the bed and with its back to the slope. This is a natural position which even a man will take under these conditions. Where the benches were wide enough, or on ridge tops, there was no uniform direction of facing except to turn the back to the wind if it was particularly strong or cold.

Day-beds are frequently used over and over again by the same or other deer, and are often worn bare of vegetation from continuous use. While lying in their beds, they nibble at any forage within reach on the ground or overhead, so the sites are usually picked clean.

Axis deer always lie down by folding their forelegs under them first, then their hindlegs. They get up on their hindlegs first when arising. They can rise and be running so rapidly when frightened that it seems they are almost exploded out of their beds and into full stride. Nor-

mally, however, they get up slowly, arch their backs and stretch their legs luxuriously, and then move off.

When lying down, they usually have their legs folded under them in readiness for quick flight, but they sometimes roll over onto their sides with legs extended in complete relaxation. Their resting attitude is one of dozing rather than sound sleep, and the head is often partially erect even though the eyes are closed and the animal appears sound asleep. Even while dozing, the ears and nostrils are attuned to sound and scent, and they are wide awake in an instant at any sign of danger.

An interesting note about the bedding habits of these deer is that bucks frequently urinate in their beds while lying down. Their rate of excretion is slow enough to let the urine soak into the ground rapidly, forming a very small wet patch and hardly contaminating the coat at all. Does have never been seen to do this, so if a fresh bed is found with a wet spot in it, it is almost certain to have been that of a buck—a point worth remembering by the hunter.

Effects of Weather on Daily Movements

The daily feeding and resting movements as described are typical for normal, clear dry weather with little or moderate wind. On Lanai in the dry-land habitat, a rainy day will change the pattern and the deer will tend to remain under cover instead of coming out in the open in the evenings and early mornings to feed. The rain does not seem to bother the deer particularly ; captive deer lie or stand in rain with no appearance of discomfort and only seek shelter if it rains very hard. Nonetheless, they are rarely seen in the open during, and for perhaps a day following, rain.

In the cloud forest habitat of east Molokai, rain is an almost daily occurrence and there is no escaping it. In fact, deer and goats have been observed to move into the open during drizzles and fogs to escape the drip from the trees. There is neither a daily or seasonal movement here, nor other movement within the home range for food and shelter.

A heavy wind also seems to keep the deer under cover, particularly those ranging the comparatively open brushy slopes away from the coastal forests of large kiawe trees ; they tend to move and feed in the shelter of tree-clumps and brush-patches in the gulleys, and are not seen as abundantly in the open during the normal feeding hours. The wind itself may cause no discomfort, but they appear much more nervous and ' spooky ' during a strong blow and perhaps remain closer to cover for this reason. Strong wind dissipates odours rapidly, creates a constant sound of rattling branches, and puts all vegetation in motion, thus making danger much harder to detect. It is possible that the deer realize their senses are not as effective under these conditions,

However, on west-end Molokai there was no noticeable difference in the behaviour (nervousness) of the deer under such conditions, perhaps because they are constantly keyed-up to their highest pitch due to heavy hunting.

On cool or overcast days, the morning feeding periods last longer and the evening periods commence earlier. The deer move about more during these periods and feed longer than they do on hot mornings and evenings when they seek shade earlier and leave it later.

Foggy weather, while rare in the dry-land habitat, is common in the wet forest and just below it. Under these conditions, deer may be encountered feeding in the open at a much later hour than on clear days. On Lanai, if the fog persisted, the deer living in the lower fringes of the cloud forest often remained out, moving and feeding as long as it lasted, perhaps spending much of the night bedded down. However, on Molokai during the time which we spent on the high north-eastern open ridge in the rain forest, deer were gone from the open ridges as early as dawn on the drier slopes. Likewise, they were abroad all night long, judging from their frequent calls all around camp, and from the tracks on the trails ; and this during the nightly rains and fogs. In the rain forest where the collecting of specimens was done on both clear days as well as many rainy foggy days, there was no consistency of activity. Deer were sometimes encountered in the open during the clear days as well as in fog and rain. Likewise, during many rainy and cloudy days, deer did not appear in the clearings until late afternoon.

The stage of the moon, while not a weather condition, also seems to affect the daily movements to some degree. During full moon, feeding is heavier at night when visibility is relatively good, and the deer take cover earlier in the morning and leave later in the evenings. The reverse takes place during the dark of the moon.

Seasonal Movements

On Molokai the only seasonal change was not of movement, but rather one of activity as it was affected by water and food. With the rainy season, food and water becomes abundant and the deer are not obliged to travel to the tanks for water. Food is abundant in the open kiawe forest as well as on the open ridges. Concentrations of deer disappear from some areas near favourable feeding places—such as sections of forest with a good bean crop. They are then somewhat more uniformly distributed throughout the forest areas. Perhaps, if anything, there is less movement and activity than during the dry season. There is, of course, not even this change in activity within the rain forest.

On Lanai, as on Molokai, there is no great seasonal variation in temperature. The seasonal variation is one of rainfall and, with it, of vegetation and surface water. On the north end during the summer and

fall, when the weather is normally dry with only an occasional shower, many deer move to the upper ridges and some even move up onto the north end of the central plateau, where they spend the entire day bedding in whatever cover is to be found. They are probably seeking more succulent vegetation than that to be found at the lower elevations. Although there is plenty of green feed throughout the range all year, the almost nightly dewfall at the higher elevation may itself be the cause of the movement.

With the first heavy rains of late fall, the deer almost immediately move down to the lower elevations, where they remain throughout the rainy period and for some time thereafter. During this period of time, the deer have choice food and water within the forest cover they prefer, and so remain in it.

Sometimes during the winter there are long periods between rains and the lower elevations again dry up. When this happens, the upward drift of deer again occurs just as it does in the late spring after the main rainy season. These ' seasonal ' movements are not really shifts of the entire north-end herd, but rather a spreading of the herd during the dry periods. Although many deer do move into the high elevations, others remain on the coast and in the intermediate country. Wet weather concentrates nearly all of the population in and near the lower forests.

This spreading and retracting of the herd in relation to the weather cycles is noticeable primarily in the population occupying the north-western, northern, and north-eastern slopes of the island, where there is moderate to heavy forest at the lower elevations. The forest attracts the deer because of its favourable cover, food, and water when conditions are favourable.

There appears to be no major upward movement along the eastern coast in dry times, possibly because of unfavourable food and cover conditions higher up, but more likely because water is available along this coast all year in the form of sump-units, seeps, and a few pipe-line troughs all within the heavy forest.

Along the southern and western slopes there is no coastal forest to hold the deer during the rainy season. Here they occupy all parts of the slopes the year round. The most noticeable change in activity is that during the wet season there is less use of the pineapple field margins than during the dry season. We see, here as elsewhere, that water is the critical factor that, along with cover, determines and controls the movements of the deer, both daily and seasonally.

Water Use

During the dry season, when natural water is scant, deer inhabiting sections of the islands where artificial water units are available make heavy use of these units. It is not known definitely how often individual deer

must drink, but indications are that in hot, dry weather they need to drink at least every day or two. Water units were visited with a frequency that indicate daily use and possibly more often. In the dry north-end range of Lanai, where no artificial units are available at present and where long trips are necessary to get to the few coastal springs, seeps, and potholes, they probably drink less frequently. A captive deer was able to get along for several days without drinking water, even in hot weather, as long as green forage was plentiful, but would use water every day if it was available. However, this deer would pass up water for days at a time if the weather was cool and heavy dews occurred. His water consumption, measured over a 26-day period of mixed hot and cool weather, averaged 2·5 pints (1·18 litres) per day—this was for a 120-pound deer.

On Lanai, in the dry north-end habitat, deer may have to make trips of up to five miles in order to reach water, though most of them travel much less than this. The ones that spend their summer at the upper elevations apparently obtain most of their water requirements from dewfall, with only occasional long trips to the coastal watering spots. However, those in the lower areas probably must water daily. One buck was collected in this habitat that had a damaged stifle joint which limited his movements severely. Although he was in an area of abundant forage and the wound in itself was not serious, he was extremely emaciated and weak due to the fact that he was unable to make the long journey necessary to get to water, and apparently had been without it for days.

In this dry area of Lanai, which incidentally contains the largest part of Lanai's deer herd, the deer make use of any potable water that they can find. This includes one or two freshwater springs found on the beach at high-tide level, brackish water seeps in the mouths of several gulches just behind the sand beach, and the several rain-water potholes which last all year only in Kaapahu Gulch on the north-western slope. They even wade out into the shallows on the reef and apparently drink salt water occasionally. Actually they are probably drinking brackish water where fresh water seeps up through the salt water in places on the reef. Such freshwater springs in the salt water are well known on Molokai, and both cattle and deer used them in days past, though apparently not to any great extent today. To what extent cattle or deer can use pure salt water is not known, but an observation made on Molokai is worth noting in this respect.

On 19 January 1957, seven of the Molokai Ranch Santa Gertrudis bulls were observed on Papahaku Beach. These were a group of young bulls, perhaps two-year-olds, that were often seen in each other's company as a bachelor group. The seven bulls walked out across the beach from the direction of the Papahaku water trough, and on reaching the water, each walked into the surf and tasted the brine. Several apparently swallowed some water. One bull waded knee deep into the surf

and drank continuously, just as if he were drinking from a freshwater trough. It was estimated that he drank at least a gallon and a half or two gallons of water judging by the length and steadiness with which he swallowed water. Drinking time lasted approximately half a minute, possibly longer. No ill effects were noted either then as the animal wandered away with his companions, or later as they were seen in the vicinity of the water trough. There was no need for any of the animals to drink salt water ; all tried it and several drank at least two or three swallows, while one drank deeply. A water trough was available within 400 to 500 yards. January is in the rainy season, and there was no dry, hot weather that might force an animal to drink salt water. Deer quite commonly wander out on the beaches. Do they drink salt water ? How often and how much do they drink ?

On Lanai the artificial water units are heavily used during the dry periods. At these units they show their characteristic suspicion and nervousness even though they must have watered there many times before, and it is interesting to watch them approach. They approach with utmost caution and hesitancy, often running off for a short distance for no apparent reason several times during the approach, then nervously returning. Once they have reached the water, the fear seems to subside and they drink with relative calm. When a group approaches the water unit, one or two will often be bolder than the rest and approach the unit first, while the rest fidget about a short distance away. When they see the 'advance guard' drinking safely, the rest will then move in confidently.

If the water unit is overflowing onto the ground and forms a puddle, the deer prefer to drink out of the puddle rather than from the trough. While at the water unit, they frequently dawdle for some minutes, taking a drink, walking around or shoving for position, and then returning for another drink. They usually leave a water unit, particularly one that is in the open, by a different route from the one by which they approached.

On Lanai there appeared to be no set time for watering ; they would visit the troughs or natural watering places at the beginning of the evening feeding period, or at any time during the night, or during the early morning before bedding down for the day. Occasionally they would come to water during the daytime but this was uncommon. On Molokai in the forest cover, the most common watering time appeared to be late afternoon and early evening, although deer continued to arrive long after dark. Papahaku trough, which was located in a heavy forest, was watched on many days and occasionally all night long. A few deer could be expected to arrive at all times of the day. These were usually singles often a doe with a fawn, sometimes a buck. Apparently these were unattached animals that had missed the normal crowd and just came in as it suited them. The big press around the trough would be from four o'clock until just after dark. By ten o'clock at night, there would be

only a few individuals about. Dawn would see a resurgence of activity, apparently many of the animals returning for another drink after a night of feeding. At the troughs well away from any cover, such as several below Mauna Loa Heights on the lee side and some on the west end, deer were never seen at the troughs during midday and, as already described elsewhere were usually gone by sun-up. Likewise, their approach here was reluctant and slow before sundown, and all drinking appeared to be done during the night, although exceptions undoubtedly did occur here also.

As soon as good rainfalls provided natural potholes of fresh water in the gullies, the deer on Lanai abandoned the artificial units and the less palatable beach supplies, obtaining their water from potholes, and rarely visited the other sources until the potholes had again dried up. They prefer to drink from muddy, stagnant pools of natural rainwater in the cover of the gulch bottoms, rather than from the clear, fresh water of the artificial troughs. Even the troughs in Maunalei gulch, which are in a dense kiawe forest, are rarely used during the wet season.

On the west end of Molokai the rainy season also brings an end to the use of water troughs by deer. The rainy season usually starts with torrential rains that turn the gulches and gullies into torrents. These flow only for a short time, the best ones for perhaps a week or so. Then the gulches are again dry. The water-holding quality of this area is extremely poor and pools of water are scarce. In a few of the deeper, larger gulches good pools of water remained over a period of several months during the main part of the rainy season. These, however, are so few that it was easy to check them often for deer use. Not one instance of use by deer was noted during the entire rainy season of 1957-58. The soft silt and mud around the pools made checking very easy and, although tracks were on several occasions found near the pools, it was obvious that the deer had only walked by the pool but had shown no interest in the water. At this time, also, no tracks were found around the water troughs. It is obvious that, in this area at least, all water requirements were being obtained from the fresh green vegetation available at this time. Rumen contents in specimens collected at this time in this area showed a very high water content—25-50% by volume—obviously more than enough to satisfy the deer's water requirements.

The water pools in the gulches dried up long before the lush green vegetation declined so that, by the time the vegetation no longer supplied the water needs of the deer, these pools of water were no longer available. As the vegetation dried up, there was a gradual increase in use of the water troughs. A similar pattern of water use was noted for the cattle in this area.

Phillips (1935), in speaking of the Ceylon axis deer, has this to say of its drinking habits : ' It generally drinks daily, towards midday, and

in dry weather is usually to be found in the vicinity of water-holes and tanks between the hours of 10 a.m. and 1 p.m.'

Trailing

When travelling to and from feeding grounds and watering sites, the deer follow well-used trails that form a network throughout their range. The feeding movements are random, without necessarily following trails but, when travelling from place to place, they usually follow trails if it is at all possible. This system of trails on Lanai reaches its greatest development in, and just above, the coastal kiawe forests, where they form a complete lacework covering all parts of the area. The trails become less numerous towards the upper limits of the range, where they lead more definitely from one point to another rather than wandering in all directions as they do in the forest. Usually trails follow available cover, crossing open areas at their narrowest points, but some cross large expanses of open grassland when leading from one feeding ground to another, or to water. They frequently follow contours of the land, but may go straight up and down steep ridges, and there is usually a series of trails in the bottoms of the gulches. Trails are particularly noticeable at watering sites where they converge from all directions.

In the Molokai rain forest range, the vegetation is so heavy and profuse, and the deer density so low, that trails are few and faint at best. Where they are noticeable at favourite crossing points, they are usually short and faint, and quickly vanish once the deer leave the crossing point.

On the west-end where cattle use is heavy, deer use the cattle trails as well as their own. On the south-west side in the quite heavy cover, trails are indefinite and show only along steep slopes or on points where deer must follow a favourable bit of terrain. Above the forest, the trails quickly converge into the cattle trails to the water troughs. It was noticed that, when leaving the forest, deer tend to drift in a loose group until well up the hill towards the trough before actually forming a trail group. Likewise, when leaving the trough, the group stayed on the heavy cattle trails only for a short distance over the roughest part of the terrain. Then they quickly spread out in a loosely grouped formation on the broad grassy ridge top for the last quarter of a mile or so down to the forest, feeding hastily or just trotting and walking as they hurried back to cover.

On the broad, open flats on the south-west part of Molokai Ranch, there were definite deer trails leading to the nearest water troughs. These were used for the specific purpose of reaching the watering site. Most were used by small groups of deer, some of which travelled up to three miles to reach water. They could not be considered heavily-used

trails since they were generally used only at night for a two-way trip by the several groups of deer that used each trail.

Well-used trails are usually trampled bare of vegetation, forming narrow ribbons of naked soil through grassland parts of the range. Within the dense forests, where the ground cover is scanty at best, they merely form beaten pathways across the nearly bare ground. Trailing appears to be the major form of range damage caused by deer on Lanai at present. This is more apparent than real, except in a few areas of concentration of small size where the ground is trampled bare. It is most common on the loafing grounds, usually within a clump of trees, where the deer may congregate and mill around. It is by no means serious. There is little evidence of erosion being caused by trailing, since most of the deer range is in an area of low rainfall. On the wet rain forest range it would take many times the present deer population to show any noticeable effect on the soil or vegetation.

On Molokai Ranch, in the area of the leeward forest below Mauna Loa, most of the forest is not used by cattle, which are excluded by fences which extend along the fringe of the forest for a considerable distance. In other parts, cattle stay above the main forest, or use only the upper edge because of the location of water troughs. Here one can see an interesting contrast between the effect of the cattle and that of the deer. Below the cattle-use area, deer trails are faint and ill defined at best ; grass is knee high in the open forest. Above the forest, the land can best be characterized by the scarred erosion gullies, erosion sinkholes, heavily tramped cattle trails, and all the other symptoms and signs of land abuse.

Home Range

Because of the poor success in capturing and marking wild deer, our information on the size of the home range and extent of movement of these deer is very limited. However, a few distinctively marked deer were observed over and over again in a relatively small area. They remained in an area of approximately a quarter of a square mile, if one can exclude the occasional long trips to special feeding areas or watering troughs. During the dry season, when seasonal movements to the upper elevations occur on Lanai, the deer appear to establish a home range within a fairly small area at this higher elevation ; most do not move back to the lower slopes for resting after feeding on the upper slopes. A few, however, may make these daily movements of several miles for water, returning to favourite resting grounds afterwards. In these cases, probably much of the feeding is actually done in these favourite areas also.

Deer residing in the sections where seasonal ' migrations ' are not necessary — such as the herd occupying the eucalyptus forest above

Lanai City — spend most of their daytime activity in an area not over one-quarter of a square mile. Their nightly foraging, however, may take them up to a mile and a half from the daytime resting areas.

Effects of Human Activity

Throughout most of Lanai's deer range, human activity is usually limited to the daylight hours. Since deer spend most of the day under cover, little effect upon their normal activities and movements has been noted. Where their range includes well-used roads, or where it adjoins the plantation, they simply move away from the disturbed portion during the time of human activity, returning at night after activity ceases. Some merely seek out the best cover at hand and wait out the disturbance if it is not too severe or too close. The small herd living just above Lanai City commonly feeds right next to a number of homes throughout the night, disregarding the barking of dogs (providing these are chained), talking, lights, and other human activities. At daylight they move back into the forest where it is quiet.

When people move directly into the deer range, the reaction is much the same as that noted near the roads and pineapple plantation. Deer frightened away by campers during the day will frequently return after dark and go about their normal activities regardless of the camp, merely remaining a discreet distance away. They often come to within 100 yards of camp and spend long periods barking in curiosity at the camp fire.

Hunting, of course, does affect the normal activities of the deer. If the hunting is light, such as one or two persons collecting a specimen now and then, the disturbed animals leave the area hastily but apparently return again at night. Heavy hunting will cause the animals to flee in all directions and, if it continues, will keep them on the move all day, forcing them into long flights from which they may not return for several days. Many seek out the heaviest cover they can find, wherein they spend the day in hiding rather than leave their home area, while others run back and forth, circling, if possible, in order to remain in country they know. Where hunting goes on continuously, as on Molokai Ranch, many people believe the deer herds move out of the area entirely for the duration of the hunting. If this were true, the west-end range would long ago have been cleared of deer. Observations show that the vacating of a particular area is only temporary and that actually most deer do not leave, but merely keep to the dense cover during the day. Where areas have been thoroughly driven and most of the deer moved out, they return again at night. Papahaku forest on the west coast was hunted every weekend, and often during the week, during the winter of 1957-58 ; yet within 24 hours after the hunt, often within a few hours, deer could be found in the forest if one cared to leave the roads to look about. The type of road

hunting usually practised here does not take the hunters into the dense thickets ; they do not see as many deer as at other times and assume that the deer have moved out.

Deer can be moved out, of course, and axis deer are particularly susceptible to driving. On Molokai Ranch it was often the practice to send a number of drivers into Papahaku forest on the south end ; these would fire ' scare shots ' as they went and this type of driving would often move deer in large numbers out of the area of the drive. These would return, usually the next night.

As a rule axis deer are sensitive to human activities during daylight hours and either leave the area temporarily or withdraw to dense cover. During the night they will put up with a remarkable amount of harassment before abandoning a choice feeding location. Attempts to keep them out of alfalfa and pineapple fields at night by means of patrols, firecrackers, gunshot, lights, and acetylene exploders have been, for the most part, futile. Shooting them at a safe range with a shotgun loaded with skeetshot was the only means found effective for keeping them away, and even after this treatment many would return in a few hours. Although nervous and fearful of the least disturbance during the day, they appear to feel completely secure and safe under cover of darkness.

Gregariousness and Herding Instincts

True herd formation, on the order of that of the North American elk or the European red deer, does not take place with the axis deer. There is, however, the rudiment, or the beginning, of such a herd formation. The axis deer does not appear to have a strong herding instinct and a group feeding or moving together will often scatter and go their own way when disturbed. Even when undisturbed, various individuals and small groups commonly leave a larger group and drift off on their own, to feed or seek resting places. This was commonly reflected in changing numbers and compositions of groups that regularly came to drink at certain water troughs. One morning one might see 40 animals, the next only 25, and the next 30 ; sex ratios and age classes would be equally as varied. This is quite in contrast to many herds of elk, sheep, and pronghorn antelope which we have observed, and in which numbers and individuals may remain very constant throughout the year except for adult males, which join the herds during the breeding season.

Gregariousness is there, and they like the company of others of their kind. It is common for small groups to rest, feed, or travel together. Single deer or small groups frequently leave their bedding spots and drift together to form larger herds while feeding. When left behind, individuals will hurry to catch up with the main group.

A captive buck, raised alone from infancy, would follow his master like a pet dog, apparently enjoying his companionship, though he would not hesitate to run off alone if frightened. Another pair of fawns, also raised by hand almost from birth—but together—were inseparable and were most unhappy if not together. These two also seemed to enjoy their owner's companionship, but to a much lesser degree than the one raised alone. The behaviour and actions of deer raised in captivity must be interpreted with caution, however, for there are many influences under such conditions not found in the wild state. Captive conditions may bring about expressions which would never be developed under wild conditions, although, in this case, the desire for companionship seemed apparent—at least for young deer.

Herd Composition and Size

The basic unit of the herd appears to be the family group, usually composed of an adult doe, her yearling fawn, and her new fawn, if she has one. If the yearling is a buck, he may leave his mother and strike out on his own as his first spike antlers mature, but it is not uncommon to see several spike-antlered bucks remaining with a group of does and fawns. The yearling does apparently remain with their mothers until their own first fawns arrive, and in some cases even after they are nursing their own young. An old doe, with a distinctive white chevron on her neck, was seen several times in the company of another doe, apparently an yearling, which also bore the same unusual mark. Both does had small fawns, one of which was similarly marked.

The larger groups may be made up of several of these family units, which may join together temporarily for companionship when feeding, travelling, or resting. Herd composition and size often change during the day and single animals may band together for a short period of time on good feeding grounds, on trails to and from feeding and watering grounds, or on favoured loafing grounds, later breaking up to go their own way. It is not uncommon to see an older buck or two moving temporarily with the doe-yearling-fawn group. These, however, usually do not remain long with them unless one of the does happens to be in season.

Except during and just after the peak breeding season, most of the mature bucks tend to seek solitude or form ' bachelor ' groups of two or more animals. This is particularly noticeable on Lanai when many of the bucks are ' in the velvet ' during the late winter and early spring months. During that period, they are often seen in such bachelor groups, or alone, and rarely with doe-fawn groups. During the peak breeding season, and for a while thereafter, the bucks join the doe-yearling-fawn herds, and groups of all ages and sexes may be seen to-

gether. But here again, the composition of the groups is not necessarily constant, since many of the bucks shift from one group to another in search of receptive does.

Due to the fact that some breeding goes on at all seasons of the year—even though the peak rut is in late spring and summer—this sexual segregation is not nearly so clear cut as it is with other temperate-climate big game. A few bucks may be seen with the doe groups at any time, probably following those females that occasionally come into season during other than the main breeding months. This situation is even more confused on Molokai, where the almost constant hunting pressure disrupts what would be the normal group behaviour pattern on less-disturbed Lanai, and causes the sexes to mix in a more random manner throughout the year.

Harem-gathering and herding by large bucks is not common with the axis deer, although occasionally a large old buck will do so to a limited degree. Even during the breeding season, the bucks are more or less outsiders in the groups and, although they may be the physical masters because of their size and aggressiveness, are rarely the herd leaders. Although leadership, like other phases of the herding instinct, is poorly developed in the axis deer, what there is of it appears to be of a matriarchal type. An old doe is usually the initiator of such action as she may influence, and often is the one to warn of danger and lead the escape, although she is probably acting as an individual rather than as a deliberate leader.

There is no basis for the commonly held belief that bucks are the leaders of the herd, or that they will protect the does and fawns from danger. When danger threatens and a group takes flight, it is rarely a buck that leads them off, but rather an old doe. The larger bucks usually follow last or run off by themselves, abandoning the others. Not only do they not protect the does and fawns, but big bucks frequently bully them, use the does when they can, and leave them to shift for themselves at the first sign of danger unless it happens to be convenient to follow them in flight.

Altogether, the herd organization and behaviour pattern is a primitive one, with poorly developed habits and characteristics of organization or specialization.

In size, the herds on Lanai usually number about seven to eight deer or less, although some are occasionally seen with ten or more. Larger herds are more common on Molokai, where 15 to 25 were commonly seen. There, one herd of 97 was observed. This was apparently made up of a number of smaller groups that left a feeding area at the same time over the same route, thus forming a large herd while travelling, but splitting up again on reaching the resting grounds. There is no justification

for the ' herds of 200 ' or even more that one often hears about.[1] Such herds are often reported on Molokai Ranch, but apparently are largely the figment of wishful thinking by those who have never been there, or someone who has driven through the area and has seen perhaps 20 or 30 deer dashing away in all directions among the kiawe bushes and trees. Such a sight appears most impressive and is quite likely to look like ' 200 ' deer to the inexperienced and impressionable viewer—especially several days later when the experience is being recounted to an equally impressionable and wishful audience.

Hunting pressure, both on Molokai and Lanai, may cause the temporary formation of larger-than-normal herds. Small groups and individuals, running back and forth to escape hunters, may join together in common flight for short periods, giving rise to the ' large herds ' often reported. Also, these large herds may be composed mainly of does, fawns, and young bucks, leading to the belief among hunters that mature bucks are scarce or ' shot out '. Actually, bucks in general, especially older and larger bucks, tend to be more phlegmatic, perhaps through longer experience, and are consequently less prone to panic and run about. These may hang back in heavy cover and hide while the hunting is going on. Thus, they may be overlooked during the hunt, but soon show up after the hunting is over and conditions return to normal.

In the rain forest of Molokai, the largest groups observed numbered five, a typical group consisting of an old doe, a younger one, two yearling does, and a 16- to 18-month old spike buck. Other groups of two to three and four were the rule.

Prater (1935) has this to say of numbers and activity :

> ' They are seen in herds of ten to thirty, which may contain two or three stags ; but assemblages numbering several hundred have been met with. They do not shun the proximity of villages, enter cultivations and frequently associate with many forest animals, particularly monkeys. They are less nocturnal than sambar and feed till late in the morning and again in the afternoon, and lie down in the interval in some shaded spot.'

Apparently the Hawaiian axis deer have not changed much, for there is little that we can differ with in this regard. Perhaps the Hawaiian deer are not quite so tolerant of other animals, but then there are few with which to get acquainted. The feeding in India seems a bit late in the day, but then again as we have seen, there is some variation even between Molokai and Lanai.

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[1] Mr. E. R. C. Davidar, The Nilgiri Wild Life Association, at p. 682 of Vol. 61 of this journal publishes a photograph of a ' herd ' of axis deer, which he estimated as consisting of more than 500 individuals.—Eds.

Curiosity

Unusual occurrences or objects, if not recognized as immediately dangerous, excite the strong sense of curiosity (or anxiety) in the axis deer. When they see something they don't understand, they stare at it intently, with neck stretched out, ears up, tail up, and all muscles tense and ready for immediate flight if necessary. If nothing 'dangerous' happens they will watch for some minutes, barking their '*yowp*!' of curiosity or mild alarm, then begin to approach guardedly, or to circle downwind to get the object's scent. While approaching or moving about for better views, they are as tense as tightly wound springs, lifting each leg quickly and nervously. They usually raise their front legs high and stamp each forefoot down hard, as though to ensure a solid footing for a quick flight—however, quite possibly such an action telegraphs a warning sound to other deer, — or could it be a threatening gesture?

A group of deer attempting to satisfy their curiosity in this manner form a picture of tense concentration, high-strung fear barely concealed by burning curiosity. The least disturbance or sound will cause the group to scatter like wind-blown leaves. If the sound or disturbance is minor and does not appear dangerous, they will often stop after a few leaps and again begin the cautious approach. Finally, their curiosity satisfied, they almost immediately forget their concern and begin again their normal feeding. One or two may keep a close watch on the strange object as they move off, and occasionally one will return for a second or third close inspection.

Usually, an observer standing motionless in view of a group of deer will hardly be noticed as long as he is motionless. A quick movement will focus every eye upon him. If the movement is not repeated, they soon forget their fears and resume their normal activities. Repeat the movement a time or two and one will soon circle downwind to get the scent, whereupon there is a startled '*yup*!' and one and all vanish in a drumming of hoofs.

The reader must not get the impression that standing motionless will always conceal him from recognition. Experienced individuals do learn to recognize the human form—and vehicles. This is particularly true on the much-hunted west-end of Molokai. In the picturesque and beautiful Papahaku forest, a parked jeep, even though carefully backed into what was considered a most favourable position for blending concealment, was recognized as dangerous, and produced instant flight when the deer were still 60 to 70 yards away. Likewise, the observer was readily recognized even though completely motionless. Association and conditioning is the primary factor here.

Older bucks in a group will usually stand quietly in the rear, watching intently but not approaching, allowing the does and younger spike bucks

the opportunity—and possible danger—of discovering the nature of the object or occurrence. These old-timers are satisfied with watching from a safe distance or, if alone, perhaps by circling downwind at a safe distance. If they do not determine the nature of the strange object by a few minutes of staring, they usually slip quietly away rather than risk a closer approach.

Curiosity will sometimes get the better of them, however, and they will react in much the same manner as does and younger bucks. A group of deer, including a beautiful, full-grown buck with polished antlers and swollen neck, several smaller bucks, and a dozen or so does and fawns, was stalked for photographs as they fed near a clump of kiawe trees on Lanai. When within about 50 yards of them, the observer —who had crawled on his stomach through the grass and low brush— carefully raised himself and set up camera and tripod. These movements were made while partially screened by brush, and were made with great care ; furthermore, the observer was dressed in a camouflaged parka to help break up his outline. While he was setting up, the deer became aware of the slow, guarded movements, but were unable to recognize the form as being human, or for that matter, as anything else of immediate danger.

Their curiosity was intense, however, and they began the typical nervous pacing, all the while staring at the unknown object with necks stretched and tails raised, and uttering their ' alarm ' bark back and forth. The big buck, who had been standing back in the cover of the trees and watching quietly, finally could stand it no longer, and he, too, moved out with the others to bark and to stare with neck stretched and raised to its utmost. After a number of photographs had been taken, the building tension grew too much for them and the whole herd whirled and vanished in the forest.

People are often tempted to ascribe greater sagacity to the large bucks but, although they may certainly be somewhat wiser than young animals because of more years of varied experience, their actions may also be due to other factors than true intelligence. The males, particularly the old males, of most members of the deer family are not of the same temperament as females or young males. There is by the very nature of maleness, especially mature maleness, a greater degree of stability, self-assurance, and what may pass for better judgment but may only be less excitability.

Energy and alertness are largely directed towards one goal—breeding activities—and are expended in this direction. A great deal of energy and aggressiveness must be available to accomplish this in the type of rutting behaviour found in the members of the deer family, more in some than in others, true, but a great deal in all. This also calls for what we, for lack of better knowledge, call a more phlegmatic nature between

breeding periods. Such a condition is not compatible with an excitable, nervous disposition.

A buck that stands quietly and does his viewing of a suspicious object from a distance without a great to-do may be no more stupid, or for that matter any smarter, than his nervous sisters. Also, he will probably learn just as much. Likewise, it is doubtful that he is deliberately letting his females and junior members do the dangerous work for him. Not having the nervous temperament of the females and younger animals, he is usually content to do his viewing from where he is.

Three captive fawns raised on Lanai all showed strong curiosity about their surroundings. Their fear of humans, at least of certain individuals that they knew, had largely been overcome. Their true character was readily observable and was not hidden or modified by the factors that influence the life of a deer in the wild.

All three closely examined everything within reach, particularly in relation to edibility. Almost every object had to be sniffed, licked, and, if chewable, chewed though not necessarily swallowed. Strange objects in the pen were always approached and examined, even though some nervousness and fear may have been expressed at first. Strange animals were likewise subjected to intense examination, though much more guardedly.

Two small goat kids were placed in a small pen adjoining the fawns' pen for two days. The fawns, which had never seen a goat before, were at first very hesitant and remained as far away as they could but, shortly after dark the first night, they approached the kids with the usual mixed fear and curiosity. After 'stalking' carefully up to within 15 feet of the goats, they stopped. The next hour was spent in barking at the goats while examining them from this 'safe' distance, all the while exhibiting the usual signs of deer curiosity: head stretched as far up and forward as it would go, ears forward, eyes staring, nostrils flared and searching, tail held rigidly up and flared wide, and forefeet stamping as they slowly stalked stiffly back and forth. At the end of this time, the fawns apparently decided that the kids were probably nothing to fear, but not really to be trusted. They then moved off to another part of their pen and settled into their regular routine of grazing and resting, keeping some distance away from the goats, but hardly looking their way again.

Reaction to Fright

When deer are watching something because of curiosity, but are unable to satisfy themselves that it is harmless, the tension may build up to the breaking point and they may jump into hasty flight. If they

are not too frightened, they may stop after a few hundred yards after putting some cover, such as a ridge, gulch, or large clump of trees, between themselves and the danger. However, if thoroughly frightened they usually run for a half-mile or more before seeking cover in which to stop.

One of the most interesting aspects of flight in these instances is their orientation to the wind while fleeing. They will almost invariably run into the wind if it is at all possible to do so. So strongly established is this safety orientation that they will frequently run into the wind even when it involves the risk of passing closer to the object of their fear. For example, groups of deer have on many occasions been observed to circle close by, or angle towards an observer, the object of their fear, in order to run into the wind ; yet there was ample room to run in any one of several other directions that would have taken the deer away from him. On several occasions deer actually overran the observer, i.e., they passed on either side within a few feet of him when actually they could more easily have avoided the danger by taking the opposite direction or several other directions, all away from him.

This commonly observed display is probably not only an instinctive orientation, but is also related to the habit of these deer to panic easily. The instinctive reaction to wind direction is there and, when sudden fright occurs, they may panic so suddenly that they automatically take the direction into the wind even when it is to their disadvantage. Such witlessness under conditions of sudden fright is quite striking in comparison with many other ungulates.

When danger threatens, or a deer is suddenly surprised, it usually utters a single startled yelp of warning. This sound, a short, sharp '*yowp*!' is uttered only once and is almost always heeded, resulting usually in instant flight by all within hearing. This can be well illustrated by the actions noted during another photographic stalk, this time of a buck that was heard calling from a ridge-top in the kiawe forest below Mauna Loa, Molokai.

A careful approach brought the photographer to within 60 yards of the buck—a superb specimen in full breeding condition in the midst of a group of does, fawns, and lesser bucks which were spread out among the trees. These were resting and dozing while the 'master buck' kept repeating his rutting call and horning a kiawe limb. The observer, partly concealed behind a tripod and movie camera, was quietly running off film when the buck stepped out from under his tree and walked towards the camera, completely unaware of man's presence.

As he stepped into the open about 40 yards away, the sight of the camera and tripod and whatever showed behind it, and possibly the quiet hum of the camera motor, struck his senses. The pop-eyed astonishment, but, unfortunately, not the startled squawk of alarm, was

clearly recorded on the film, as was also his lightning-quick about-face and disappearance into the thickets. There was no hesitating, no curiosity, and no second-looking here.

When thoroughly frightened, deer rarely stop for a second look, but keep running at full speed until well away, and only then stop for a brief look back ; more often, they simply slow down but keep on going until they feel safe. Bucks, possibly because of their less excitable nature, occasionally stop for a second look if they are not certain of the cause of the alarm.

Both bucks and does will tire quickly after the initial all-out blazing burst of speed and drop to a slow run and then a trot, occasionally stopping to make a check on the pursuit or danger. As they become exhausted they seek cover in which to stop to hide and rest, leaving it reluctantly if closely pursued, only to dive into other cover.

The axis deer do not lie as closely as do the blacktail, mule deer, or white tail deer. Only occasionally will they lie so close that one can pass but a few yards away. However, when exhausted and very frightened, they may take refuge in very dense cover, if it is present, and refuse to move so long as they remain undiscovered. When dogs got into the experimental range-pen where two does were penned and killed one of the deer, the 15-acre pen was combed with 14 drivers to remove the dogs left in the enclosure. This enclosure, roughly rectangular, contains a heavy rain forest cover of ferns, shrubs, and trees over about one-half of the area. Two drives, one lengthwise and one crossways, with 14 yelling, brush-beating boys netted two dogs, but no deer. It was assumed that both deer had been killed by the dogs and that one probably was killed in the heavy brush where it was difficult to see. However, a few days later the doe turned up safe and sound in the pen. She had obviously crawled into one of the many heavy thickets, overgrown with the almost impenetrable staghorn fern, and let the drivers pass by.

Does are especially prone to panic and, when cornered, or when they think they are cornered, or when very badly frightened, they may go completely to pieces in blind panic, running into objects in their way, or over cliffs, injuring or killing themselves. Once panic grips them, they run until it leaves them or, if they cannot get away, they run back and forth into whatever barriers are present, battering themselves until they drop from exhaustion or injury. Under these conditions they frequently die from shock. If caught by man or dogs, their panic wells up in loud bawls of abject fear ; otherwise they run in silence.

Cornered bucks will try every means of escape, including charging their tormentor in an effort to gore and overrun him. Unlike the does, they are not as likely to lose control of themselves. When all hope is gone they may lie down and sulk, waiting for an opportunity to escape

or fight. The Lanai investigator was very nearly gored by a buck on Molokai which was discovered tangled in some light field telephone wire. One end of the wire was thoroughly tangled in the buck's antlers, while the other end was snagged in a clump of kiawe trees ; thus the buck was on a 50-foot line like a trout on a hook. When approached, he ran into the grove of trees to the limit of his line. When he was further pursued, he immediately whirled and charged at full speed with antlers lowered. Quick footwork saved the day by inches, though the investigator was flipped over by a trailing loop of wire. The buck was soon subdued by means of a drugged dart, ear-tagged, and released.

As already stated, the deer become more confident after dark and do not take fright as easily or readily as during the day, nor do they permit fright to overcome them as easily. Even the scent of humans may cause them to run off only a few yards before stopping. They apparently depend heavily on the protection of darkness rather than on flight, and feel secure. Noises and actions that would send them into a panic during the daylight may startle them at night, causing them to run off for a short distance before stopping, but will only rarely put them into wild flight.

When attempts were being made to frighten them from the pineapple and alfalfa fields at night by means of acetylene ' cannons ', firecrackers, and gunshots, they soon became accustomed to the noise and would all but ignore it. Often they were spotlighted with a powerful light while rifle shots cracked over their heads and into the brush around them in attempts to drive them away. The usual reaction was to jump and fidget at the first few shots, then to move off a short distance, and finally, if the shooting continued, to trot over a ridge or into a ravine out of sight, all the while showing obvious reluctance to leave. The same actions during the daytime would bring on a wild and immediate flight.

Even under normal conditions, when not attracted to some choice location by food (such as under drought conditions which were involved in the cases mentioned), they nevertheless are more reluctant to leave the area of disturbance at night, but do so in a relatively calm manner, compared with daytime behaviour. When spotlighted, they do not usually 'hold' as well as do some of the other deer species, but fidget about nervously, attempting to get out of the blinding glare. Once out of the light, they soon settle down unless very badly frightened by close approach of a human, or by the sting of a drug-laden dart hitting them. At this they will immediately run and keep going until out of sight in good cover. This is the main reason why this method of capture has so far failed ; once they are hit and really scared they do not hesitate to leave the area at full speed, night or day.

This paradoxical behaviour of the deer by day and night may not be

as easily explained as it appears to be. To say that the deer 'realize' they cannot be seen and feel secure is easy, but an analysis of this simple explanation leaves much unanswered. How can the deer know they cannot be seen? If they themselves can see well, as is indicated by their freedom of movement at night, then they must also see man and his activities at night. On the other hand, if their security lies in not being seen, then our assumption that they see well must be false. For the only way that a deer could feel that it was not seen (to be hidden) is not to see well itself. It has no knowledge of how well we see, but only of how well it sees. The answer may well lie somewhere between the two extremes.

We ourselves do not rush about at night because of our limited vision. The same is probably true of the deer. While there is little doubt that deer and other ungulates see quite well at night, the visual acuity may well be relatively short and, while the animal may see very well within reasonable limits which would enable it to get around with ease and to forage for its food (keep in mind a highly developed sense of smell, vibrissae to help in tactile sensing, and sure footwork), it may actually be operating in a visual field that is not very large. In other words, rather than feeling altogether secure, it may simply be more reluctant to go barging about in a world in which its own vision and perception is much more limited than during the day. Be this as it may, there is apparently some feeling of safety at night which leads it to wander into areas which it would not enter during daylight. Our knowledge of the night vision of wild animals is extremely limited, and we need to know much more before we can analyze their night time behaviour correctly.

There is another possible explanation for the lack of continued fear over loud noises during the night, and the use of exploding devices, gunfire, etc., may be the wrong method entirely for scaring deer during darkness. It has already been pointed out that when sense perception is not associated with a known danger, then no fright reaction will result from the sense stimulation. We assume that since deer do run from sounds of gunshots during the daytime, they will react similarly at night. Under cover of darkness, and with the possible inhibition of visual senses, deer may simply accept the repeated explosions of carbide exploders and guns as a natural phenomenon, such as thunder, rather than related to man. Deer readily become accustomed to dynamiting and similar continuing activities. During the daytime there is no difficulty in keeping deer out of crop areas such as the case mentioned because they can see that man is associated with the disturbance. It should be possible to do so at night by providing the right stimulus and sense association to produce the desired reaction.

Swimming

Axis deer swim well when forced to do so but, in Hawaii at least, they do not enter the water by choice. Several have been encountered on the shore where they were trapped between the sea and impassable cliffs, perhaps having fallen into this situation or driven into it by feral dogs. None of these was observed to attempt to swim out of their predicament; they would walk back and forth disconsolately, looking for a way up the cliffs. Perhaps others, not discovered, have saved themselves from starvation by swimming to freedom voluntarily. At any rate, when attempts were made to free those that were discovered trapped, they readily entered the sea and swam strongly away. One, at least, was drowned by being caught between a sheer rock ledge and the pounding surf while attempting to regain the shore. A few reports have been received of others seen swimming off shore but no details of the circumstances are known.

Play

Wild fawns have frequently been observed playing wild, carefree, running and butting games, and all three captive fawns showed a strong desire to play when well fed and secure from danger. Play takes the form of leaping back and forth, wild, zig-zagging runs through the brush, and mock head-butting fights. The captive fawns frequently chased each other around until they were panting from the exertion, and seemed to enjoy the 'game'. Male fawns apparently prefer the butting games, while the females prefer the running games of 'tag'; although both sexes will engage in some of each.

Both captive male fawns enjoyed playing butting games with their owner; this consisted of butting his outstretched hand, arm, or foot as rapidly and as hard as they could, alternating the actual butting with a comical, high-jumping, back-and-forth dance, somewhat like a boxer practising his footwork. As they grew older the play became rougher and, by the time 'Willie', the first fawn, developed his spike antlers, the owner was hard put to keep up with his play. After Willie's spike antlers matured and hardened, his playfulness began to give way to aggressive anger and he became too dangerous to rough-and-tumble with.

While playing, the tail is held up with the hair flared out, presenting a striking white 'flag', and the infra-orbital scent glands are frequently opened wide in excitement. This play, besides being an enjoyable means of using up excess energy, undoubtedly also serves as valuable training for the fawn's future life by hardening muscles, teaching foot-work for running and jumping, and preparing the young bucks for their adult battles.

Adults of both sexes have occasionally been observed to engage in similar games, though such instances do not appear to be common, especially among older animals. Several times, particularly during cool mornings or evenings, does have been seen chasing each other wildly in play, and, once, a spike buck and a doe engaged in a game of tag, including some mild butting and shoving, apparently all in a spirit of play. Spike bucks, with both mature and velvet-covered antlers, commonly engage in mild sparring contests with each other, apparently more in playfulness than in anger.

Older animals appear to lose their 'sense of humour' and not only refuse to play, but intervene in the game of others if they come too close and annoy them. On one occasion, two fawns were seen chasing each other merrily around the brush. Their play took them near an old doe, which was browsing on a klu bush; as the fawns ran by her, she whirled, charging at them with forefeet striking and teeth reaching, immediately breaking up the game. On several other occasions, mature bucks jabbed with their antlers at small fawns that played too close, or that came up to sniff them in curiosity.

Social and Territorial Behaviour

The aggressive and bullying nature of the bucks becomes evident when they are still fawns and increases as they grow older. The two captive fawns that were raised were inseparable friends; even so the little buck did not hesitate to butt the doe out of his way to get at preferred food or to keep her from getting petted when he wanted the attention. As bucks grow older and develop spike antlers, they become even more aggressive and frequently use their weapons to bully and shove does that get in their way.

The relationship between males of various ages in the axis deer appears to be one of rather primitive and unspecialized development compared with that of other cervids with a highly specialized and well-developed herding characteristic.

In the axis male there is the normal aggressiveness and antagonism that is common to males, but it is far less segregated in terms of age classes and seasons. This shows up in the very generalized year-round breeding cycle and potency of the bucks, as well as the much milder antagonism and animosity that bucks show towards each other at all stages of their relationship to each other and to the does.

The general attitude of bucks of various ages and stages of antler development follows a pattern that is not unusual or unexpected in such animals. Larger animals dominate smaller ones, and older animals dominate younger ones. Hard-antlered bucks generally dominate those in the velvet, although here social order may assert itself when a large

old buck in the velvet comes up against an immature buck with hard spike antlers. The authority of habit and the size and years will give the older buck right of way over the younger one even though the 8- to 10-inch needle-sharp spike antlers could be a most potent weapon for the young buck. This is all as is to be expected. Within these general rules there is, however, a good deal of variation as well as an over-all tolerance of adult bucks towards the younger ones and each other in general that is not observed in cervids of more modern groups.

Spike bucks commonly engage in shoving and sparring contests with each other, many of a playful nature, but others in a more serious tone. These sparring matches begin when the antlers are still in the velvet, indicating that they are not as tender as is sometimes believed, though they do appear to 'pull' their punches to some degree at this time. These spike bucks often give the appearance of being the most aggressive of all ages, since they commonly may be seen stalking around with their hair all bristled up, challenging any other buck near-by. They approach each other, stalking stiff-legged like two strange dogs, pawing the ground, and hooking at brush; then may come a contest as they put their heads together and begin to shove back and forth. Such battles usually end in a draw, and both contestants quit almost as though on a signal and resume their feeding. Sometimes there may be several of these contests going on at one time in a group of bucks, and at times even a three-way match.

Such behaviourisms are usually accorded the most common interpretation of the simple expression of aggressiveness or simply competitive animosity. However, in many cases there may be quite complex underlying aspects of social structure and organization, varying in degree of development and significance.

This underlying social structure is the 'territorial and signpost' behaviour pattern. We have already mentioned the home range. This is the area in which the animal feeds and lives. Within this, or perhaps overlying this, there may also be a territory which the animal will defend against encroachment by others of its kind or, if not defended, at least it is not invaded actively by others. The first would appear to be the more primitive, the latter the more developed and specialized. In the case of an undefended or ' psychological ' territory, it would have to be carefully and definitely marked out with recognition signposts which could and would be recognized by other individuals. In its highest development, these signposts would have to have an intimidating effect in the absence of their marker for the greatest effect and usefulness. The making of signposts, i.e. the activity itself, may also have an intimidating effect on a potential invader or competitor.

Most members of the deer family show this territorialistic behaviour to some degree. Observers have recognized it in some form, usually

without a knowledge of its significance. In most cases little is ever said about it, and for that matter, very little is known about most of our deer in this respect. One of the best developed territorial behaviourisms is that of the Roosevelt elk, with its interesting and highly ritualized and spectacular signpost habits (Graf 1956). Others (Lindsdale 1953, Darling 1936, *et al.*) have recorded signpost behaviour, with either no comment on its real significance, or without recognizing its significance.

As a rule, a well-developed signpost habit indicates a well-developed territorial habit and a complex social structure. The axis deer shows some of these to a degree, mostly weakly developed and not highly organized. Its signpost habits, though well developed are only moderately organized so far as any apparent benefits are derived. However, this may only be our lack of understanding and interpretation.

There appears to be no territorial segregation of herds, and as already described, the herds are rather loosely organized and not too stable in composition and numbers. Animals do have an area in which they prefer to stay and where several, perhaps a family group, are found ; one could speak of these as a herd home range. Throughout these areas there will occur 'signposts' with varying frequency. This signpost is an inverted V mark made by scraping the ground with the forefeet. It will invariably be found at the base of some small plant—a small ilima or a lantana bush or even tall weeds. The characteristic 'marker' plant is never large—usually with a stem not over pencil diameter, often much less. The plants are usually not more than 18 to 20 inches high, and often are solitary ones out in the open. Sometimes the end of a low-hanging branch of a tree may be used.

The buck, and only bucks have been observed in this act, walks up to a 'marker', lowers his antlers, and brushes them through the twigs with a back and forth motion, sometimes with an up-and-down swing. After the antler-brushing, there is a careful nosing of the twigs brushed, that is running the nose carefully over the effected twigs as though inspecting them by scent. This may be done five or six times; then he scrapes the ground alternately with each front foot several times, then brushes his antlers through the twigs again. The whole procedure may be repeated four or five times at one point or only once or twice. The buck may then move on to another point ten or fifteen feet away and repeat the process.

As many as six to ten of these signposts have been found in a distance of 75 to 100 feet—apparently made as the buck wandered along ; others have been found scattered at random within a radius of 30 to 40 feet. They are often most common around the loafing and resting areas. All were found on ridge tops or on flat areas, some on feeding areas ; the latter were apparently made during the feeding period. One buck was observed to stand on his hind legs and brush his antlers through the twigs

of a kiawe tree. Most interesting here is the fact that this buck and most others observed in this act were in the velvet or were young bucks, usually spikes or two-pointers, that is bucks in their first and second sexual cycle. One is tempted to say this is the ' non-combatant ' group and most likely to benefit from this expression. However, this may be putting it in anthropomorphic terms.

The ' inspection ' of the ' marker ' behaviourism is also often carried over to the more commonly observed horning, or fighting of trees and shrubs. After horning an object, the buck often ' inspects ' the object with his nose by carefully running his nose over the horned area. ' Willie ', the pet buck on Lanai, would always do this after one of his bouts with a post or shrub. This would appear to relate at least some of the horning and fighting of trees and shrubs, and even the ground, to the signpost behaviourism although the scrape marks are omitted. Some of this behaviour is, on the other hand, only a form of ' punching bag ' fight practice.

In the axis deer, where bucks start brushing antlers in the vegetation and twigs while still in the velvet, the picture may become even more confused. The reason may be due to the fact that these deer are sexually potent throughout the year, regardless of antler or neck condition.

In the case of the spike bucks' threatening and sparring behaviour as described above, there may be more involved than simple animosity. Behaviour has been observed which takes on a uniform and ritualized posturing. It varies only slightly from that already described. Young bucks in the velvet display it more often than others. In this case, two bucks approach each other, back slightly arched and body held stiffly, neck bowed and head held low and with chin tucked in, ears flat. The tail usually, but not always, is held stiffly erect or cocked to one side. The bucks approach each other to within about 3 feet, facing, but several feet to one side of each other. In this position each one scrapes with alternate strokes of the front feet, forming the typical inverted V mark. There are usually 3 to 4 strokes in this scraping. The bucks may then circle around each other in the same relative position, walking in this same humped-back pose, with neck bowed, dorsal hair erected, and chin held in, so far as walking will permit this. The pace is stiff and with slow-motion deliberateness, almost like that of fixed mechanical figures. After circling slowly and deliberately, they may stop and again scrape the ground several times, then circle again. This may go on for four or five minutes after which the bucks will withdraw, and wander about only to come together again later and repeat this process.

The V marks are, of course, numerous at such points, but are not to be confused with those made in relation to some ' marker ' plant as described above. These latter are readily recognized by the uniformity of shape and without the trampling over them. They are located

Graf : Axis Deer

'Sign post' mark made by axis buck. The 'marker plant' can be seen to the left of the apex of the scrape mark

(Photo : William Graf)

individually and almost always with the apex just in front of some small shrub plant, or clump of weeds which will show unmistakable signs of having been worn by the brushing of antlers through it.

These behaviour patterns should be kept in mind when reading of, or observing, the various patterns of behaviour that we have described here. What may appear to be a simple antagonistic or fighting behaviour may have an underlying social behaviour origin with some significance which we do not yet fully or correctly understand. What goes on in the mind of an animal, and how this mind and its processes work, is even less understood than the outward manifestations which we observe.

The behaviour of the spike bucks described earlier may be a variation of the formal posturing ritual, and the posturing undoubtedly has some relationship to the ' signpost ' performance. The psychological effect of such rituals and performances is that they may avoid active conflict, or may minimize it—expression of feeling and accomplishments may be attained in this way and thus reduce, if not eliminate, the necessity for active bodily conflict. It may be a process of ' debate ' or of ' cold war '.

It must be remembered that in other deer, where there is a definite seasonal breeding cycle with a quiescent period, the usual animosity and aggressiveness towards each other disappears in the male ; likewise it becomes much more exaggerated during the rutting period. In the axis deer, breeding in both males and females continues during all times of the year and males are, in effect, in the rut regardless of other physiological factors involved. If the male axis deer were to display the same degree of aggressiveness and animosity throughout the year as the elk or the red deer, he would probably be reduced to a complete physical and nervous wreck. A more moderate and milder social relationship is therefore the rule. The continuous breeding condition nevertheless influences the behaviour throughout the year.

Spike bucks, therefore, will try to take on a larger buck and, while the old bucks are generally intolerant, they make no effort to go out of their way to pursue or overcome these young upstarts. The youngsters quickly learn that the old-timers are better armed and not very playful. There are exceptions to this, which illustrates the very nature of the more tolerant relationship. For example, a spike buck was observed to engage a much larger buck, perhaps three years old and of medium size with fully developed antlers. The match obviously was strictly in play with good-natured fencing and sparring and mild pushing. However, as the pushing increased, the weight of the bigger buck quickly proved to be too great for the youngster, and he was pushed back. As the younger one gave way there became apparent a rapid change in the attitude of the bigger buck, so that as he advanced his aggressiveness became more and more pronounced. Instinctively stimulated by the winning forward movement, the big buck suddenly drove forward with full force, almost

driving the small spike buck to the ground. The spike, however, instantly realized his disadvantage and turned sideways, letting the big buck slide by and so disengage himself. As soon as the youngster dodged away, the larger buck calmly walked off.

These two bucks engaged in this play several more times, usually without the larger one taking advantage of his size and weight. Only when the small buck gave way would the big buck's action build up into a forceful aggressive drive. Had the small buck failed to break off the action instantly, the larger buck probably would have built up such a vicious aggressiveness that he would undoubtedly have gored the smaller antagonist, even though the action started as play. Most of the younger and smaller bucks stay out of the way of the very large mature bucks, who are usually ill-tempered and intolerant.

The older males do occasionally engage in 'friendly' shoving matches, but usually they keep out of each other's way, bristling as they pass but stepping wide of each other. They have learned not to ask for trouble unless they really mean it. Several shoving contests have been witnessed between large-antlered bucks in the velvet, but these appeared to be merely practice sessions, with both contestants putting their antlers together slowly and gently before pushing. In one of these matches, the shoving got a bit rough and apparently sparked that instinctive anger so near the surface in these engagements, whereupon the two bucks, both in the velvet, reared up on their hind legs and boxed vigorously with their forefeet.

The bucks are in breeding condition throughout the year ; however, the psychological and certainly the physiological peak of the rut is reached only during a part of the year, corresponding to the seasonal appearance of the rut in other deer. This can be spoken of as the ' true rut ' in the axis deer. During this period the buck's neck is swollen, his antlers are hard and his ego is at its peak as is his aggressiveness. During this period, serious fights do take place, but no death-duels have been observed, nor have we found any dead bucks that have been killed by fighting. That the battles sometimes are quite rough is attested to by the scars and cuts about the neck and head of bucks examined, and one buck had a half-inch of antler tip embedded in the thick fibrous connective tissue under the skin of the neck, apparently with no ill-effect.

To fight to the death requires both an aggressive desire and a defensive willingness over some common ground or reason. In the Rocky Mountain elk and its relatives, this reason is the harem, and only the defence or pirating of a harem can bring on a fight to the death. This is lacking in the axis deer. There are no fixed or acquired harems to fight over as a rule ; there is no definite territory to defend, or if it is defended it is done psychologically. Consequently, any fight simply stems from male animosity and whatever degree of anger that may flare up sponta-

neously. An ordinary fight can at times flare up into a real heated battle that generates its own energy, though this is rare. The fights, though sometimes ferocious, appear to end as soon as one buck discovers he is being out-fought, whereupon he quickly gives up and moves off, with the winner not following up—for here there is no reason to follow up just as there is nothing to gain by staying in the fight when losing. In this respect the fights resemble those between bachelor bulls among elk—not serious, just sparring jousts, sometimes very rough but never vicious. In contrast, those fought over a harem are all out, vicious fights with no quarter given or asked, and often end in serious and fatal injuries.

It is interesting to watch the aggressive behaviour of a group of bucks just before the main rutting season, when they are still travelling together in bachelor groups. Although no actual contact between animals may take place, and they remain warily out of reach of each other, each appears to be carrying a 'chip' on his shoulder, daring one of the others to knock it off, but secretly hoping that no one will. If strange bucks approach the group, all will bristle up and stalk stiff-legged about in the usual threatening attitude, the newcomer advancing slowly in the same manner. As they mix, there may be some shoving and sparring, or they may just threaten and bluff each other for a few minutes before again settling down to feeding in relative peace. Their action here, as was also noted around the watering troughs and at other meeting places, reminds one of a group of strange male dogs approaching each other.

The threatening attitude of the axis buck is most interesting and is a most ferocious-appearing display. The hair on the neck and body is raised as in a fighting tomcat, making them appear larger, the tail is partly raised and held cocked sideways with the hair flared, heads are tilted partly sideways and the chin is tucked in, antlers jutting. Their face wrinkles up, with the lips curled back in what can well pass for a snarl. Then, with scent glands spread wide open with the inner tufts of oily hair sticking out on each side of their face, ears laid back, and eyes rolling up wildly, they begin to stalk back and forth slowly and threateningly with legs held stiffly and hind-feet dragging the ground at each slow step, all the while giving forth low hisses with each breath. This display may last some minutes before actual contact is made, if at all, and may include pawing the ground with front feet and hooking at brush or grass with the antlers.

This aggressiveness, though reaching its climax during the peak breeding season, is by no means limited to it. Larger bucks, when carrying mature polished antlers, regardless of the time of the year, are in their physiological rut. These bucks, certainly know their superior position and do not hesitate to bully smaller bucks, does, and fawns when they wish to. Their presence during a time other than when a majority of other bucks also are in this condition, places them at an even greater

advantage over other bucks which have their antlers in various stages of growth and in the velvet.

Aggressive behaviour is not nearly so pronounced among does and is rarely observed; they appear to get along in relative harmony most of the time. At times one will become annoyed by the actions of another whereupon she will strike with her front feet or bite, rarely butting with the head. The captive doe-fawn occasionally vented her spleen on her companion, or the owner's dogs, by running up and quickly grabbing a mouthful of hide and hair and giving a sharp tug. The dogs, especially, appeared to be much more wary of this approach than they were of the playful butting of the buck fawn.

Co-operation

The only observed indications of co-operation among axis deer have been limited to reciprocal licking of the head and neck, usually by two does. Pairs of does have several times been observed to stand facing each other while vigorously licking each other over the head, neck, and shoulders. It is not known whether these were unrelated females or whether they were mother and yearling daughter. The latter is perhaps more likely, since mothers frequently lick their fawns all over, with fawns licking their mother in return. When the captive fawns were being scratched about the head and neck—which they greatly enjoyed—they returned the favour by licking the arm of the person scratching them ; this appears to be an instinctive action between mother and fawn—and perhaps between any individuals. It is, in fact, possibly the explanation for the mutualness of this act. In other words, it may be a way of saying ' scratch me please ' ; that is, by initiating the licking of a certain part of the neck, or head, or other part of the body, the animal can in turn get its own part licked. Horses do this regularly ; the Roosevelt elk (Graf 1956) does likewise. In these cases, the interesting thing is that the initiator of the act gets the same corresponding part of his anatomy 'scratched'; if he nibbles or licks the right side of the neck, he in turn gets the same spot on the right side of the neck nibbled or licked. It appears to be a simple way of getting a job done without much explaining or complex communications.

Another type of co-operation which occurs, possibly involuntarily, is a form of ' baby sitting ' by does with young fawns. This is well known among other deer and also other ungulates. On several occasions one doe has been seen with two or more small fawns, although only one appeared to be her own. Later, another doe or two would join the single doe and the does and fawns would move off together, the indication being that the extra fawns had been left in the 'care' of the first doe. This could be unintentional, of course, since does often travel in

groups and, while the fawns are resting, one or more of the does may leave the group leaving her fawn just as she would when alone. Thus, the fawn is left in the company of the other does until its mother returns. Fawns that leave their resting place during the absence of the mother will then, of course, join the other fawns and does near-by.

Deer and Fences

Although physically capable of executing high jumps the axis deer, by inclination and its normal running and moving habits, is not a high-jumper. They rarely jump over a fence which lies in their line of travel, preferring to slip through or under it. Though physically capable of easily clearing a four-foot fence, they nearly always follow it until they find a spot where they can crawl under or slip between the wires. Where fences are found on their range, their trails invariably lead to places where they can go under or through the fence. When hard-pressed, they will run up to these crossings and dive under or through the fence with hardly a break in stride. Captive deer can sometimes be held within a six-foot fence of woven wire, but if badly frightened they will jump over it.

The important point here, from a fencing standpoint, is that a five- or six-foot fence would keep deer within a wild range, except for an occasional rare individual that might have special inclinations for high jumping. Deer do not jump fences just to be jumping. Such activity takes special effort and, unless there is some reason or enticement, they do not do so. On the open range, if one wanted to confine these deer to a certain part of the range, this could undoubtedly be done with a five-foot hog-wire fence. At special points, where a jump possibly might be made easier by the terrain, a single strand of barbed wire above the fence should be sufficient to discourage such attempts. Close confinement will force animals to attempt acts that they normally do not attempt.

Behaviour towards Other Game Species

Only on Lanai is there an opportunity for the axis deer to encounter other species of big game than the wild goat. When the pronghorn antelope were released on Lanai, several encounters between the antelope and the deer were observed. These encounters occurred during the early morning as the deer were moving downhill towards cover after a night of foraging higher up. As the two groups discovered each other, they would stop and stare intently with great curiosity mingled with fear. The deer would move a few steps and stamp their feet as they do when uncertain. The antelope would instantly wheel and run off

a few yards, snorting and flaring their 'powderpuff' rump patches, then stop and stare and then begin a slow and cautious advance toward the deer. This behaviour would be repeated each time the deer moved —the antelope running when the deer moved, the deer freezing when the antelope dashed off—until the tension finally built up to the point where the deer would break and run off, with the antelope hesitantly following. In all cases observed, the deer were the first to give in to fear and run away. Later, as they became accustomed to the antelope, they would feed calmly near them with only occasional signs of nervousness.

The ranges of these two species overlap only slightly, so encounters between the two are not too common except among those few deer living within the overlapping areas.

Mouflon sheep, introduced on Lanai several years earlier, occupy the same range as do the deer and meetings are not infrequent. Several such encounters have been witnessed, but only after the two species had been together for some time and had grown used to each other's presence. The deer would regard the mouflon with mild alarm and curiosity as they approached each other, perhaps stamping their feet, lifting their tails, and giving a few barks of alarm. The mouflon paid little attention to the deer, feeding along calmly, and the deer would soon get over their own apprehension and return to feeding, both groups intermingling in harmony.

The range of the wild (feral) goat on Lanai lies above that of the deer for the most part, and the two species are not commonly seen together. On the few occasions when they have been seen to meet, they appeared not in the least concerned about each other and went about their business calmly, each more or less ignoring the other. Both goats and deer have been on the island for many years, and have had ample time to learn that each is harmless towards the other.

On Molokai, wild goats and deer are found occupying the same range in the east-end rain forest. No opportunity was had to observe meetings between the two. Undoubtedly they do at times come together but probably avoid each other. Goats are by nature phlegmatic and calm, not given to excitable behaviour. The deer undoubtedly exhibit their usual nervous and excitable nature that is so characteristic of them.

Deer occupying ranges where they would never encounter goats would probably act much as they did when first seeing the antelope at the first meeting with these strangers. The two captive fawns were much concerned when two small goat kids were placed in a pen adjoining theirs, and did not get over their nervousness in the two days that the goats remained. If the goats had been kept for a few more days, the fawns would probably have overcome their fear completely.

Unfortunately, up to this time no observations have been made of

any of these competing species meeting at a water hole, where competition for a common need would be strongest. It would be interesting to see which would dominate, or if they would drink together. The latter is most unlikely in view of the highly nervous nature and complete timidity of the deer and the fact that they do not drink when cattle are at the troughs. This also would place them last on the list so far as any dominance is concerned, a position the goats or mouflon are much more likely to take in view of their generally stable and relatively calm nature.

Cock pheasants have been observed to wander within a few feet of deer, with neither pheasant nor deer paying any attention to the other.

Reaction to Domestic Animals

There is no domestic livestock on Lanai at present, with the exception of a few privately owned saddle horses. These are pastured in areas out of the general range of deer habitat, so no opportunity was had to observe reactions between these animals on Lanai. On Molokai, however, deer share common range with both cattle and horses. Horses are in the minority and encountered only over a very small part of the range. In most cases observed, the deer always showed their generally suspicious and nervous character and preferred to remain aloof from the cattle and horses. At times they have been seen to mingle with cattle and horses particularly on choice feeding areas.

In Papahaku Forest when the ripe kiawe beans were falling, cattle, horses, and deer were found together in the same area. However, the deer avoided close approach to the cattle and horses. At the water-trough, deer quickly vacated the near vicinity and permitted cattle to take over. In areas well removed from cover, they appeared very reluctant to come in very near troughs being used by cattle and would often hang back several hundred yards.

On the far west end of the island where cattle were very common on the deer range, cattle were tolerated but avoided. Close approach, such as even 5 or 10 yards, was not observed, the deer usally moving away as cattle approached within 20 to 30 yards. In some of these areas, it was noticed that the approach of cattle through the forest, even though open forest, was almost always certain to alarm and put deer to flight. The deer seemed to feel most sure of their neighbours where they could keep them under full view and clearly see what was coming and what they were doing.

In one instance, a herd of 15 to 16 deer, consisting of does, fawns, and several bucks of various ages, was observed feeding on a low ridge at sundown. A lone range cow came wandering over the ridge, and although this was in an area where cattle were common, the deer all

stopped and showed a great deal of concern, barking and staring intently and anxiously at the cow. An inexperienced and new observer would have concluded from their action that this was the first cow the deer had ever seen. These deer stopped their feeding, which had been in the direction of the cow, and finally retreated. The cow never got closer than about 150 yards. It should also be mentioned that this herd of deer had come up out of Papahaku Forest where they had daily contact with cattle and had undoubtedly associated, and even perhaps competed with cattle for the kiawe beans. This again illustrates the unpredictable nature and extreme nervousness and timidity of these deer.

Above Halawa Valley on the east end, there are a few wild cattle that still roam the lower part of the range inhabited by deer. They have been observed to associate side by side with no apparent discord. In one instance, an old cow was observed entering a small clearing in a remote part of the forest, shortly to be followed by a doe and then a fawn about six months old. The doe, perhaps 25 to 30 yards from the cow, was not concerned, but the fawn was nervous and suspicious of the cow and hung back until the cow left. In the one instance where a saddle horse was used as a 'blind horse', that is by means of which it was hoped to be able to approach deer for close observation, the ruse did not work. The deer bolted at the first sight of the horse. This was close enough to Papahaku Forest, where horses were often near the water tank, so that these deer undoubtedly had seen horses at some time in the past.

Deer in Captivity

Three fawns were raised by the Lanai investigator to obtain data on fawn development and behaviour. They were all captured when very young and raised on a bottle in a pen encompassing his yard. One, Willie, was raised along until he was about 18 months of age, whereupon he was sent to a zoo. The other two, Pepper, a male, and Squeekie, a female, were captured in the summer of 1960 when only a few days old and were hand raised to approximately five months of age, when they too were sent to the zoo.

Willie was raised without the company of his own kind, but in close company of humans and two pet dogs; he quickly became very tame. Up to the time he was about three months old, he was not penned but was allowed to roam at will, spending the nights in the washroom with a pet mongrel and a German short-haired pointer dog. He wandered about the yard nibbling at vegetation and resting in the shade of the trees during the day, occasionally following the dogs off on their neighbourhood forays but always returning at bottle-time. He quickly

learned his name and would come running when called. He always enjoyed his owner's company and attention, and liked being petted and played with. He was afraid of most strangers at first, and particularly of children. He was insatiably curious about all happenings around the place, tried to eat anything remotely edible, and especially enjoyed getting into the house at every opportunity where he would beg scraps in the kitchen, nibble papers, clothes, and cigarette butts, and generally make a nuisance of himself. All in all, however, he was an affectionate, playful, and very interesting pet while young.

The other two fawns were raised together and this had a tendency to keep them somewhat wilder, though Pepper was also affectionate and playful. The little female, Squeekie, never showed the desire for human company exhibited by both bucks; she would come readily in answer to her name for her bottle and would submit to some handling, but otherwise made no attempt to attract attention or show affection. Neither of these fawns showed the close friendship towards the dogs that Willie did, and both were much more afraid of strangers. Nevertheless, both were playful and attractive pets.

As Willie grew older and began raiding the neighbour's flower gardens, it became necessary to pen him in. However, the pen was not too substantial at first and he escaped several times. Usually he would return by himself, but once he was found several miles from home, apparently having tried to track his owner's jeep through the pineapple fields. This was not unexpected since he would become very upset when his owner would drive away, and would attempt to follow the vehicle. Another time he was gone for 11 days and, as was discovered, had joined the herd of wild deer inhabiting the forest edges above Lanai City. This occurred after his spike antlers had matured, and the mating urge first appeared. The owner finally located him feeding with some other deer several miles from him, and when his name was called he came trotting like a lost dog. The others, of course, fled. Then he followed the jeep home, and appeared happy to be back in his pen. During his freedom he had obviously tangled with some larger bucks and had found that he was neither as big nor as tough as he believed, and had gotten a few scars in the bargain for his pains.

As his antlers matured and he began to lose the velvet, Willie showed the normal characteristics of a maturing buck and—what can be expected of all male deer in captivity—he began to get decidedly aggressive and antagonistic and dangerous towards anyone entering his pen. This is characteristic of buck deer raised as pets; they lose their fear of humans and, when they reach their first breeding season, become pugnacious and dangerous, and will continue to be that way from then on. The captive deer, Rudolph, owned by Mr. Noah Pelelo Sr., was raised much as Willie and was kept in captivity until he was 11 years old. His

pen could be entered only when his antlers were newly shed or still very young. As soon as they had reached near full size, he would immediately charge anyone standing near the fence, even though his antlers were still soft enough to tear and bleed near the tips. During his captivity he put two men in the hospital with serious antler wounds. It is well to remember this.

In the wild, bucks are never dangerous towards man under normal circumstances but, once tamed and without the overpowering fear of man, the natural instinctive antagonism and combativeness are turned towards the nearest object at hand. People are not recognized as friends, but as antagonists, and no distinction is made between men and women. Once a buck attacks a man there is no discouraging him, and few have any chance of winning out against the brute strength and implacable rage of a buck with the battle lust upon him. A full-grown buck is more than a match against a man; it takes the most powerful of men to handle even a yearling buck, and then it is not certain that he will escape uninjured. We know of several instances of men killed by penned deer, and the keeping of male deer is most inadvisable. They make interesting and beautiful pets when young, but become exceedingly dangerous when they grow up. It is, therefore, wiser to refrain from raising them unless for reasons of study and research.

Although all three fawns were raised in close association with humans and they all became reasonably tame, they never lost their natural nervousness and instinct for survival. Sudden or unusual occurrences would make them fly into a panic, causing them to run wildly back and forth in the enclosure, leaping into the fence in their efforts to escape. When in such a state, they seemed almost blind to obstacles, running into anything in their way. This appears to be typical of axis deer when badly frightened, and the fawns plainly showed how quickly and thoroughly their instincts would overcome the thin veneer of tameness.

Fawns, raised in captivity by their own mothers (who themselves may have been hand-raised or captured in the wild) and which have a minimum of handling and attention, never become tame. These fawns remain as timid and shy as the wild deer. The deer belonging to Mr. Pekelo have already been referred to in this respect. His buck, Rudolph, was reasonably tame and not easily frightened. The does and fawns would fly into a complete panic when approached by strangers, charging blindly and repeatedly into the walls and fences of their shed and pen often injuring themselves. These are deer that have spent their whole life in captivity in quite close association with humans, but because they were not individually hand-raised on a bottle like Rudolph they never overcame their natural fears.

The axis deer, raised for several generations in the Honolulu Zoo,

respond in the same way. They tend to remain at the rear of their enclosure when visitors are watching, and are continuously nervous and watchful and never get completely used to people. Paul Breese, Director of the Zoo, states that they are the most nervous and excitable of any of the wild animals he had handled.

Handling Captive Deer

Axis deer, whether wild caught or 'tame', that must be handled for weighing, tagging, etc. are a problem. They can put up a terrific fight and must be subdued by force ; however, if handled too roughly they may die on the spot from shock. The best method found so far is by means of nets ; two or three men can carry a large net into a trap or pen, herd the deer into it one by one, and wrap them up rapidly and with relative ease with little chance of injury to either party. They can then be weighed, tagged, and handled without hurting themselves and, what is most important, apparently without suffering from shock.

Tranquilizing drugs have been used with some success in helping to handle axis deer. It was found that Thorazine, injected intramuscularly at the rate of 0·5 mg. per pound, calmed one buck and one doe to some degree, making them much easier to work with. The drug Librium has been tried several times on the captive fawns, but has shown little effect other than to make them weak and wobbly without calming them in the least. The dosages tried have been orally administered up to a rate of about 2·3 mg. per pound of body weight. More work is needed before the success of these and other drugs can be determined, but they appear to promise an easy way to reduce the self-inflicted injuries and death from shock when handling captive axis deer.

REPRODUCTION AND DEVELOPMENT

Breeding Cycle

The breeding and fawning season of the axis deer in Hawaii, as in other parts of the world, is not limited to a clear-cut season of the year. Blandford (1888-1891), Lydekker (1898), Prater (1935), and Phillips (1935) all mention the irregularity of the fawning and antler-shedding in the Indian axis deer.

The indefiniteness and direct contradiction of these writers indicates how little is known today about the Indian axis deer. Recent extensive correspondence with various members of the Indian Forest Service, the Zoological Survey of India, and private individuals who kindly undertook to check some of these matters for us confirms the fact that the axis deer there has no regular breeding and antler-shedding season though, as in Hawaii, there appears to be a peak season. It is of interest

to note that a temperate climate does not affect the cycle of these deer. Whitehead (1950) states that the axis deer in England breeds at all seasons of the year, and that 'the majority of calves would appear to be dropped between Christmas and Easter'. Heck (1935) has the same to say about the axis deer in Germany.

It was not possible to determine with absolute certainty all the factors related to the breeding cycle and its various phases both in bucks and does. However, in general it can be stated that fawns are produced at all seasons of the year with a peak fawning period from about the middle of November to April. Likewise, antlers are dropped at all times of the year, but the peak period of dropping corresponds roughly to the early part of the fawning season. Peak antler-maturation and breeding or rutting activity occur from about April to August, though breeding by any mature buck can take place at any time of the year regardless of the stage of antler development in which he may find himself.

Just as there apparently is no inhibition of breeding ability during the antlerless period in a buck, there apparently is no inhibition of the estrus cycle of does by lactation. The indication is that a doe may come into breeding condition within a few months after having given birth to a fawn which she will be nursing. These two factors must account for the irregularity or non-seasonal breeding of these deer. The fact that this does not alter even in temperate climate indicates an inherent physiological characteristic and not something that is caused by the tropical climate in which these deer are normally found.

In a temperate or northern climate, the young of deer must be born in the spring to survive. This is ensured through a mechanism where the breeding cycle is inhibited in the female during lactation or simply through a regularly spaced cyclic estrus period to ensure coincidence with the season. A similar cyclic quiescence in the males further ensures this coincidence with the seasons. In the axis deer the bucks can breed at any season of the year, and does apparently have a repeated estrus period with such frequency that no definite breeding season will become established.

The acclimatization of true temperate zone deer, such as the European red deer and others, in a climate where the seasons do not coincide with their own breeding cycle will result in an adjustment of the breeding cycle to fit the season. This is the situation in south-temperate New Zealand where the seasons are the reverse of the natural range of many of the deer introduced there. The north-temperate climate animals now have a breeding season just the reverse of those in the north-temperate zone. (Donne 1924, Wodzicki 1950).

We have no explanation for the failure of the axis deer to adjust itself to climatic conditions even in such unfavourable climates as England and northern Europe, other than that offered.

Temperature in Hawaii does not vary greatly; however, there is definitely a seasonal rainfall variation, and in this respect the main fawning season or peak corresponds to the season of maximum rainfall. In India, the best information that we have been able to obtain indicates that the fawning peak falls somewhere between August and February; however, there is some conflict of information on this. The consensus of information indicates that there is at least a weak correlation with the monsoon or wet season there also. The indication is that the coincidence of these seasons and the fawning peak may be just that—a coincidence rather than an adjustment of the cycle to the climatic conditions which happen to be favourable. If this were not so, then the seasons should have had a profound influence on the breeding and fawning activity of these deer in the cold temperate climates where they have been introduced.

Favourable climatic conditions, whether temperature or moisture and food or all of these, will of course have an important effect on the survival of young animals. This in turn may tend to group the arrival of most of the fawns during these favourable months. As will be seen later, bucks apparently shed their antlers with great regularity. It would be most interesting to know whether does have any regularity of recurring pregnancy—it would appear not at first glance; however, we do not have enough data to be certain. The breeding cycle in Hawaii may be just a carry-over from that originally developed in India. The median dates of the varied information received from India would fit our season close enough.

It will be interesting to see what change, if any, takes place in the reproductive habits of the newly introduced pronghorn antelope over the years. This species has a well-defined breeding and fawning season which does not coincide exactly with optimum conditions in Hawaii.

Antler Development

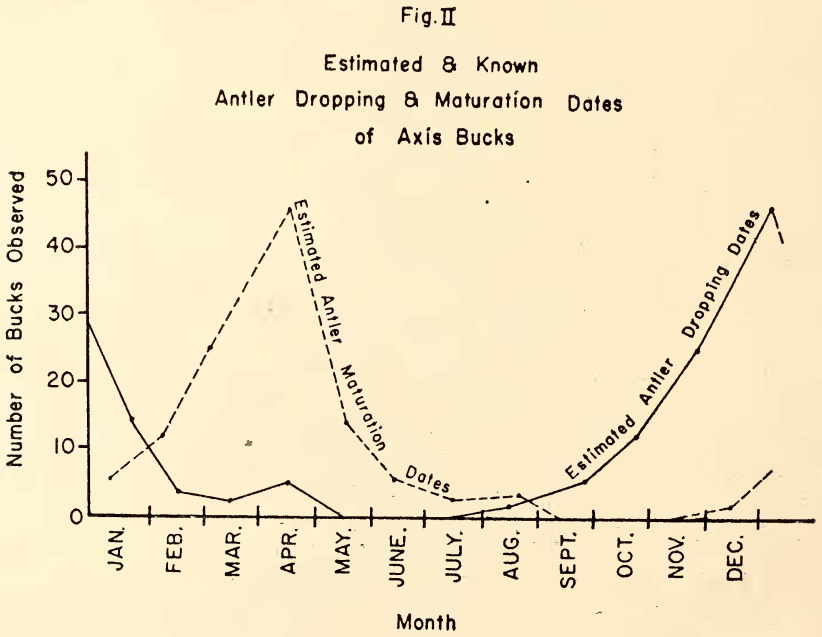
Closely associated with the rutting season is the development of the bucks' antlers; in fact, rutting activity begins with maturation of the newly-developed antlers, and the beginning of the major rutting season may be determined by discovering the period when most of the bucks shed the 'velvet' from their new-grown antlers.

During the course of the present study, close watch was kept on the captive buck, Rudolph, on Molokai, in order to determine the length of time required to grow a set of antlers. This old buck was very consistent from year to year in dropping his old antlers and developing his new ones. The first two years he was checked he dropped his antlers on the same date, January 7; the next year he missed this by only one day, dropping them on the 8th. In the first year, the antler scars on

the pedicles were completely healed over and new growth was evident 17 days after he dropped his old ones. The second year, it took only eight days. The antlers were mature, and began peeling or shedding on May 18th both years. Thus it took 132 and 130 days respectively, or a little over four calendar months, for new antlers to become completely developed after the loss of the old ones, which he carried for nearly eight months.

In order to arrive at the approximate period when most wild bucks shed the velvet from their antlers, the antler-dropping dates were estimated for all bucks observed in the velvet for two years. The state of their antlers was compared to the observed growth-rate of the penned buck, and by working backwards, the approximate dropping date was obtained. This data is plotted graphically in Figure II, which shows the estimated month in which each buck dropped his old antlers. Assuming that antler development in most bucks roughly follows that of Rudolph, taking a little over four months for completion, the corresponding curve to show antler maturation dates was also plotted in Figure II. These two curves indicate that the majority of axis bucks drop their old antlers in December each year, and that most of the new antlers are mature by April.

Fig. II

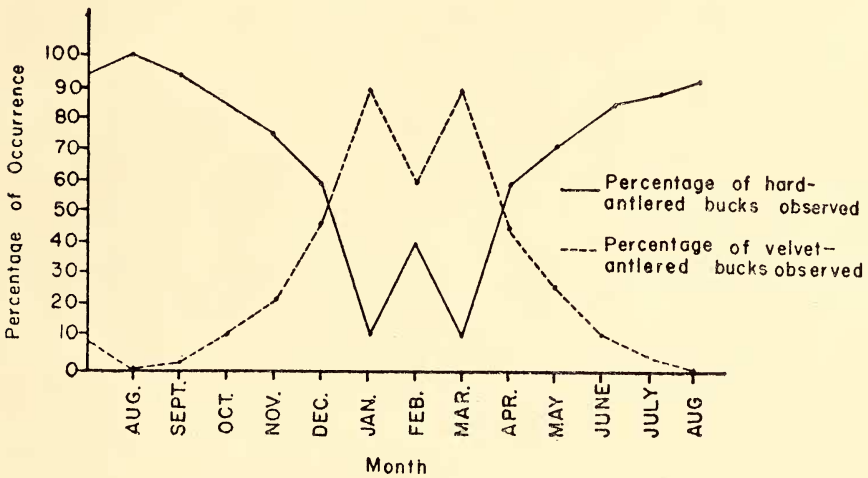


In order to corroborate these two periods, the curves shown in Figure III were constructed by plotting the percentage of occurrence of all bucks observed each month with hard antlers versus all seen with

antlers in the velvet. The curves show a sharp drop in bucks seen with hard antlers in December and a sharp rise in April, again indicating that the majority drop their antlers in early winter and develop new ones by mid-spring. It must be remembered, however, that although the bulk of the bucks follow this pattern, many are 'out of phase', and some may be seen in any stage of antler development at any time of the year. It is not at all uncommon to see a few bucks that have

Fig. III

Antler Condition By Percentage Of Occurrence And Month



just shed their old antlers, or that are in the velvet, during the summer, or bucks with mature, polished antlers during the winter.

After they have lost their old antlers and while new ones are developing, most of the bucks travel together in bachelor groups apart from the doe-fawn groups, although they may occasionally mix with these while feeding. A few of the older stags may even become solitary, keeping apart from others of their kind. Bucks in this state appear to realize the loss of their armament, and become even more shy and nervous than usual. They stick close to cover and keep out of sight as much as possible, taking to their heels more readily when alarmed.

When the antler is dropped, the surface of the pedicle is left raw and open and may bleed slightly. This 'wound' is quickly covered with a soft, greyish blue skin, and in one to two weeks new growth in the form of a slight knob is noticeable. While the antlers are growing—which they do from the tips, not the bases—they are covered with a thick, soft skin, which has a coat of fine, short, velvet-like hair, giving rise to

the term 'velvet'. This protective skin contains a well-developed circulatory system which provides blood and nourishment to the growing bone beneath. Damage to this skin or velvet while it is still functional causes severe bleeding and, if the damage is sufficient to impair circulation to the growing tip of the antler, malformation or stunting may result. It is not uncommon to see bucks with clubbed or twisted antlers, probably resulting from injury while they were developing.

Such injuries are not hard to visualize since many bucks engage in mild to moderately rough sparring contests while their antlers are still developing. As their velvet-covered antlers begin to mature, the bucks' confidence and belligerence returns, and signs of antagonism are exhibited. Several weeks before Rudolph's antlers were fully mature, and while they were still soft enough near the tips to bleed when struck, he began jabbing and gouging them on the fence in his efforts to attack onlookers.

At this stage of their antler-development, the bucks reach their best physical condition and build up an abundance of visceral fat. With the final maturation of the antlers, their necks begin to swell; the skin over the sides and upper portion of the neck becomes thick and tough, and a thick, subcutaneous layer of connective tissue develops in this area. The neck muscles become enlarged, providing the protection and strength needed for the more strenuous battles to come.

When the antlers reach full maturity, circulation in the protective skin is much reduced or decreases altogether and the skin dies, drying into a fibrous, paper-like covering. As it dries and splits, it peels down and off the antler in long shreds and strips. The process is fairly rapid so that in a period of several days the buck may be left with tangled strands of this dried skin hanging from his antlers and over his head and face. Some bleeding may occur from parts of the skin not completely dried, but it is minor and merely stains the antlers to varying degrees with the brown of dried blood.

The common assumption that bucks remove the velvet by rubbing the antlers on shrubs and trees is not entirely correct. Actually, the velvet comes off naturally and without help, though, obviously, the rubbing that does occur will help to remove it even though rubbing may not be done for this purpose. At the time when the velvet is drying and beginning to peel, an instinctive desire to rub their antlers arises, perhaps being encouraged by itching as the velvet dries, but more likely by the excess energy of the fully-awakened rutting urge. The bucks begin to spend numerous periods in thrashing small trees and brush with their antlers, sometimes calmly and deliberately, sometimes in apparent rage. Such rubbing does help to remove shreds of velvet—though not deliberately—and also stains the antlers more fully, as well as covering them with bark fragments and other debris.

Breeding Ability and Pregnancy Rate

Although the outward signs of the rut are most apparent in the period following the maturation of the buck's antlers, which for most of the bucks is in late spring and summer, and although most of the breeding takes place during this period, bucks apparently are able to breed successfully at any time of the year. Several observations have been made of wild bucks breeding receptive does after the bucks have dropped their antlers. The pet buck, Rudolph, was recorded as successfully impregnating a doe two days after dropping his antlers on January 7th, over eight months after he actually began his rutting season.

A number of bucks were collected in various stages of antler development, ranging from those that had just lost their antlers, through those with partly developed antlers in the velvet, to bucks with polished antlers but apparently past the peak of the rut. Microscopic examination of the reproductive tracts revealed that mature and active sperm were plentiful in all cases, indicating that the animals could impregnate a receptive doe at any time of the year, regardless of outward appearances.

Bucks without antlers, or in various stages of velvet, do breed with does not uncommonly as our own observations show. It would seem reasonable however that, where bucks with hard antlers are present, these would do the breeding in most cases, since they would have no difficulty in fending off their unarmed rivals from a receptive doe.

Little has been learned about the sexual activity and the estrus cycle of the axis does. They appear to be receptive to the buck for only short periods of their estrus cycle, not unlike other deer. They apparently go through several estrus cycles annually, though how many is not known definitely. From the little evidence that we have, it would appear the great majority of does are bred the first time they come into heat on reaching sexual maturity, and thereafter are bred as they come into season after the birth of each fawn.

The only observations so far available by which we can estimate the length of the doe's estrus cycle were made on a pair of captive deer. The buck was observed to mount the doe on September 19th, then again on December 9th and December 16th. The September 19th act can be considered as an unsuccessful breeding. The second two dates, however, present several possibilities. Either the buck forced himself on the doe prematurely, that is before she was actually in full estrus, which might be possible under pen conditions, or the axis deer has a long heat period. In any case, the December 16th breeding was successful and the doe became pregnant. No more mounting of the doe was observed after this date. The time lapse between the first and second breeding was 81 days, and between the first and third 88 days. Since our records in

these cases depended on the observations of the owner of the animals, one can only make assumptions as to the estrus cycle. If the doe went through regular estrus cycles between the first breeding attempt and the last one, one could, on the basis of a 27-30 day estrus cycle of similarly sized deer, assume that she had gone through three cycles between September 19 and December 16 or, if no other estrus periods occurred, then it is possible that the axis deer may have an estrus cycle of approximately 85-90 days, which is not too likely. Since we do not know whether the doe was kept separated from the buck between the first and third breeding (normally the practice by the owner) this remains pure speculation. It is a field that needs more study and observation.

Records of the time-lapse between parturition and re-impregnation of axis does are also scarce. Those obtained from the zoo showed that the four does observed again became pregnant four, four and one-half, seven, and nine months after giving birth to fawns. There is a strong indication that does often become pregnant even sooner than four months after giving birth. One doe collected had a fawn with her that could not have been more than 3 months old. This doe was carrying a 25 mm. fœtus, which can be estimated at about 50 days of age. She was from the wet rain forest, where food conditions are at their best, and the fawn can be considered to have made a maximum growth. Thus, by the most liberal estimate based on dry-land growth, breeding must have occurred here only one and one-half months after parturition, and possibly even sooner.

Another young doe, which could have been no older than 14 months according to her teeth, was found to be nursing a fawn while she was carrying a fœtus which was about 80 days old. This means that she was bred the second time at about eleven and one-half months of age. Subtracting the approximately seven to seven and one-half month gestation period of her nursing fawn from this age, indicates she was bred the first time at four to four-and-a-half months of age—and this with no time lapse between giving birth to her first fawn and being bred again. Assuming one-half to one month between parturition and re-breeding, she would have had to be only three to four months old at her first breeding. Thus, it appears that the interval between parturition and re-breeding could have been only one month at the most, and probably less, since it is highly unlikely that she could have been successfully impregnated before she was three or four months old. Even this age must be an exceptional minimum for sexual maturity.

Ten other does were found to be both pregnant and lactating. According to the age of the fœtuses carried, they had been pregnant from 2·3 to 6·1 months approximately, or an average of 3·6 months for the 10 animals. Since it appears that fawns are normally weaned between four and six months of age (and probably closer to four months)